Volume 30 MAY, 1956 Number 3

PALEONTOLOGY

JOURNAL OF PALEONTOLOGY

UNIVERSITY OF MICHIGAN

JUL 23 1956

MUSEUMS LIBRARY

A publication of The Society of Economic Paleontologists and Mineralogists *and* The Paleontological Society *with the generous support and cooperation of* The American Association of Petroleum Geologists *and* The Geological Society of America

CONTENTS

The evolution of some Upper Cambrian and Lower Ordovician trilobite families ..... *Christina Lochman* 445
Some Carboniferous productid brachiopods; New South Wales .. *K. S. W. Campbell* 463
Early Ordovician nautiloids from Virginia .... *A. G. Unklesbay* and *Robert S. Young* 481
Upper Cretaceous and Early Tertiary nautiloids from Western Australia ..... *Brian F. Glenister, A. K. Miller,* and *W. M. Furnish* 492
Type and other species of Odontopleuridae (Trilobita) ..... *Harry B. Whittington* 504
New Pennsylvanian brachiopods ..... *G. Arthur Cooper* 521
A new insectivore from the Oligocene of the Wind River Basin, Wyoming, with notes on the taxonomy of the Oligocene Tenrecoidea ..... *Jean Hough* 531
Upper Cambrian trilobites; western Wyoming .. *Charles R. DeLand* and *Alan B. Shaw* 542
Ancestry of the coralline algae ..... *J. Harlan Johnson* 563
Tertiary anacanthin fishes from California and the Pacific Northwest; their paleoecological significance ..... *Lore Rose David* 568
The type species of *Litocephalus* Resser, 1937 (Trilobita) ..... *Allison R. Palmer* 608
Microstructure of the plates in the carpoid echinoderm *Paranacystis* ..... *Kenneth E. Caster* and *Theodore H. Eaton, Jr.* 611
The North American anthracotheres ..... *J. R. Macdonald* 615
Identifying fossil and Recent barnacles by the figures in the shell .... *Ira E. Cornwall* 646
Notes on the Nucinellidae (*Pelecypoda*) with description of a new species from the Eocene of Oregon ..... *H. E. Vokes* 652
Variation and tooth-replacement in a Miocene mylagaulid rodent ..... *Craig C. Black* and *Albert E. Wood* 672
Dendraster: a problem in echinoid taxonomy ..... *D. M. Raup* 685
Conodont genus *Prioniodus* and related forms *F. H. T. Rhodes* and *Klaus J. Müller* 695
Some paradoxes in taxonomy with reference to the Protista .... *Rousseau H. Flower* 700
The occurrence of Paleocene mammalian remains in the Fossil Basin of southwestern Wyoming ..... *C. Lewis Gazin* 707
Tethyan Jurassic hydroids of the family Milleporidiidae ..... *R. G. S. Hudson* 714
Ichnites from the Triassic Moenkopi formation of Arizona and Utah .. *F. E. Peabody* 731
A new echinoid from the Upper Devonian of Alberta ..... *Colin W. Stearn* 741
PALEONTOLOGICAL NOTES 712, 747
NOMENCLATURAL NOTES 760
CORRECTION 769
NOTICES 769
SOCIETY RECORDS AND ACTIVITIES 770
SOCIETY NOTES AND COMMENT 771

EDITORS

For The Paleontological Society: WILLIAM R. EVITT, Department of Geology and Geography, The University of Rochester, River Campus Station, Rochester 20, New York.

For The Society of Economic Paleontologists and Mineralogists: W. M. FURNISH, Department of Geology, State University of Iowa, Iowa City, Iowa.

The JOURNAL OF PALEONTOLOGY is published bimonthly. The issues for January, May, and September are sponsored by The Paleontological Society in cooperation with The Geological Society of America; those for March, July, and November are sponsored by The Society of Economic Paleontologists and Mineralogists in cooperation with The American Association of Petroleum Geologists.

The subscription price for the JOURNAL is $15.00 per year prepaid to addresses in the United States. Postage is charged extra for all other countries in the Postal Union, 40 cents on annual subscriptions (total $15.40). Single numbers $3.00 each to nonmembers, $1.75 to members.

Communications about the JOURNAL, advertising, subscriptions, rates, change of address, and nonreceipt of preceding numbers, should be addressed to The Society of Economic Paleontologists and Mineralogists, P. O. Box 979, Tulsa 1, Oklahoma. Claims for nonreceipt of preceding numbers must be submitted within three months of the date of publication in order to be filled gratis. Communications about membership and requests for blanks for nomination of new members should be directed to the secretary of the respective society.

Communications in regard to manuscripts or purely editorial matters should be sent to the editors at addresses above.

Authors should consult a recent issue of the JOURNAL for appropriate style and form before preparing their manuscripts. A brief, informative abstract should accompany every article except nomenclatural notes only one or two paragraphs long in which the title is sufficient to serve as an abstract of the contents. All new taxonomic names proposed in a paper should appear in the abstract.

Contributors are requested to instruct their photographers to illuminate fossils from the upper left side, the conventional manner. Plates normally should be arranged for publication at the maximum size of $5\frac{1}{4} \times 8\frac{1}{4}$ inches, exclusive of margins and heading. Printed numerals of standard size and form may be obtained free from the editors. When requesting them state number of plates and dimensions of each plate. Text-figures should be designed for reproduction at either single column ($2\frac{1}{2}$ inches) or full page ($5\frac{1}{4}$ inches) width. Typewritten copy is not acceptable for text-figures.

OFFICERS OF THE SOCIETIES

THE SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS

For the year ending March 1957

President
ROBERT S. SHROCK, Cambridge, Mass.

Vice-President
R. V. HOLLINGSWORTH, Midland, Texas

First Past President
F. J. PETTIJOHN, Baltimore, Md.

Second Past President
HANS E. THALMANN, Stanford, Calif.

Secretary-Treasurer
S. P. ELLISON, JR., Austin, Texas

Editors
W. M. FURNISH, Iowa City, Iowa
for paleontology
JACK L. HOUGH, Urbana, Ill.
for mineralogy

THE PALEONTOLOGICAL SOCIETY

For the year ending November 1956

President
HENRYK B. STENZEL, Houston, Texas

Vice-President
GLENN L. JEPSEN, Princeton, N. J.

Secretary
HARRY B. WHITTINGTON, Cambridge, Mass.

Treasurer
CLAUDE C. ALBRITTON, Dallas, Texas

Editor
WILLIAM R. EVITT, Rochester, N. Y.

Past Presidents
A. SCOTT WARTHIN, JR., Poughkeepsie, N. Y.
HARRY S. LADD, Washington, D. C.
W. STORRS COLE, Ithaca, N. Y.

Entered as second-class matter at the Post Office at Tulsa 1, Oklahoma, under the Act of March 3, 1879. Acceptance for mailing at special rate of postage provided for in paragraph 4, section 538, P. L. and R, authorized April 3, 1935.

Additional entry as second-class matter at the Post Office at Menasha, Wisconsin.

Printed in U. S. A.

GEORGE BANTA COMPANY, INC., MENASHA, WISCONSIN

JOURNAL OF PALEONTOLOGY

A publication of THE SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS *and* THE PALEONTOLOGICAL SOCIETY *with the generous support and cooperation of* THE AMERICAN ASSOCIATION OF PETROLEUM GEOLOGISTS *and* THE GEOLOGICAL SOCIETY OF AMERICA

VOLUME 30 | MAY, 1956 | NUMBER 3

THE EVOLUTION OF SOME UPPER CAMBRIAN AND LOWER ORDOVICIAN TRILOBITE FAMILIES

CHRISTINA LOCHMAN

New Mexico Bureau of Mines and Mineral Resources, Socorro

ABSTRACT—A number of monophyletic lineages are recognized among groups of Upper Cambrian and Lower Ordovician trilobites. Descent can usually be traced from a generalized ptychopariid ancestor of the late Middle Cambrian. Unlike the earlier unsatisfactory trilobite groups, these monophyletic families have a relatively short stratigraphic range, none more than 30,—40,000,000 years. In the North American seaways at three times during the Dresbachian and Franconian a major biofacies change occurred which noticeably affected the stability of the trilobite families.

A revised correlation chart of late Middle and Upper Cambrian faunal zones of northeast Asia, North America and northwest Europe is presented. A more accurate picture of contemporaneous faunas is being obtained. It is proposed that the Middle-Upper Cambrian boundary in the North American standard section be ajusted to coincide with the position of the boundary in the European section. Significant and widespread isostatic and lithofacies changes occur at this horizon in the North American sections.

Endoaspis, new name, is proposed to replace *Wutingia* Endo, 1935. *Prosaukia? anomala* Ulrich & Resser is recognized as an American species of *Mareda* Kobayashi, 1942. *Strigigenalis* Whittington & Ross, 1953 is assigned to the Lecanopygidae Lochman, 1953. A new subfamily, Iranaspidinae, of the Leiostegiidae is proposed for *Iranaspis* King, and *Plethopeltella* Kobayashi. It is suggested that *Chakasskia* Poletayeva, 1936 may be a late member of the Protolenidae, and *Inouyina* Poletayeva, 1936 may be an end member of the Antatlasiidae.

The following families are discussed: 1) The Dikelocephalidae Miller, are a small group of indigenous North American late Upper Cambrian genera derived by development of *Briscoia* from *Wilbernia*. Only *Briscoia* reached northeastern Asiatic and northwestern European seaways. *Parabriscoia* Kobayashi, 1935, is a synonym of *Elkia* Walcott, 1925. 2), 3), 4) The Ptychaspididae Raymond, the Saukiidae Ulrich & Resser, and the Eurekiidae Hupé are related families derived from a common ancestor, the generalized, highly-variable, early Franconian genus, *Conaspis*. The evolution of the families occurred in the northern Cordilleran seaways and along the western shores of Laurentia. The first two families are well represented in North American and northeastern Asiatic faunas, but the third is primarily a Cordilleran group. The status of the genotype of *Saukia* (*Dikellocephalus lodensis* Whitfield, 1880) is discussed. 5) *Hungaia*, sole member of the Hungaiidae, is unrelated to any of the above families, but is considered closest to genera like *Kainella* of the Remopleuridae. 6) *Conokephalina* and *Lobocephalina* comprise a small specialized subfamily of the Ptychopariidae. 7), 8), 9) The Dikelokephalinidae Kobayashi, 1936 are considered to be a primitive, short-lived branch of the basic stock which gave rise to the Asaphoidae. Morphologic evidences of the relationships between this family, *Eoasaphus*, the earliest asaphid, *Housia*, the sole member of the Housiidae, and the genera of the Ceratopygidae are discussed in detail. All four groups are believed derived from a common late Middle Cambrian ptychoparid ancestor. 10)

A new family—the Parabolinoididae—is erected for a group of related genera in the North American *Conaspis* and basal *Ptychaspis* zones. It contains *Parabolinoides, Bernia, Croixana, Kendallia, Maustonia, Meeria, Orygmaspis, Psalaspis, Stigmacephalus* and *Taenicephalus*. 11) The Coosellidae Palmer is revised to include only *Coosella, Coosia* and *Syspacheilus*. *Crepicephalus* is not related to this group. 12) The Pterocephaliidae range from the late Dresbachian through the early Franconian. It comprises two groups of genera, a well known North American branch, and a poorly known Asiatic one, tracing their descent from a common ancestor. 13) A new family—the Idahoiidae—is erected for a group of North American genera ranging from the base of the Franconian into the early Trempealeauan. It contains *Idahoia, Bellaspidella, Comanchia, Pseudosaratogia, Saratogia* and *Wilbernia*.

INTRODUCTION

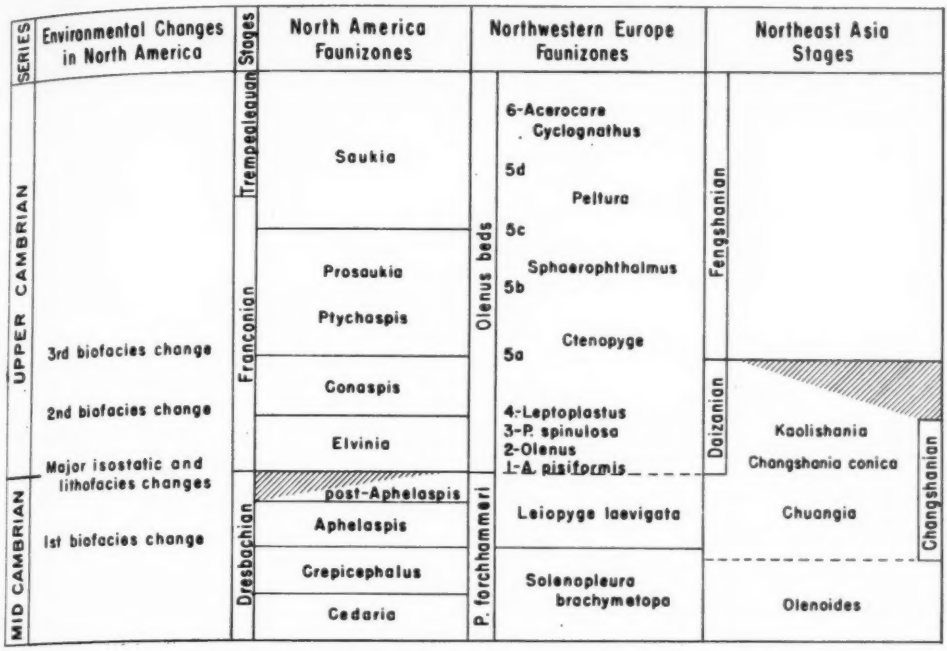
DURING the completion of work on trilobite families for the Treatise of Invertebrate Paleontology, some additions and corrections have been made, several new families and one subfamily established and one genus renamed. I recognize a number of monophyletic lineages among the groups of Upper Cambrian and Lower Ordovician trilobites under consideration.

In nearly all cases descent can be traced from a generalized ptychopariid ancestor living in the late Middle or earliest Upper Cambrian. Unlike many of the old unsatisfactory groupings, the monophyletic families have a much shorter stratigraphic range—embracing at most the Upper Cambrian, or more frequently only a portion of it; or a portion of the Lower Ordovician—a maximum time span of 30,000,000 years or a minimum of 6–10,000,000 years. During the life of a family the generalized ancestral stock gave rise to a number of progressively more specialized, short-lived genera. At three times during the Dresbachian and Franconian a major biofacies change occurred in the North American seaways, and each change noticeably affected the stability of the trilobite families in the faunas.

CORRELATION AT THE MIDDLE-UPPER CAMBRIAN BOUNDARY

A discussion of the contemporaneity of American, European and Asiatic faunas is at present hampered by the known discrepancies in the position of the Middle-Upper Cambrian boundary in the standard sections of North America and Europe. In 1939 Howell & Lochman advanced the first evidence that the *Elvinia* zone of the basal Franconian was the more exact correlate of the base of the Upper Cambrian in the European section, rather than the *Cedaria* zone of the North American section. In the ensuing years additional evidence has accumulated as the faunas of the zones have become better known in North America. A much more exact zonal correlation is now possible (Text-fig. 1). The *Leiopyge laevigata* zone of Scandinavia (Westergård, 1953) is considered the equivalent of the *Aphelaspis* and post-*Aphelaspis* zones (Palmer, 1954); the three earliest Upper Cambrian zones of Scandinavia (Westergård, 1922) the equivalent of the *Elvinia* zone; and zones 4, 5a of Scandinavia as the probable correlatives of the *Conaspis* zone in which related genera, such as *Parabolinoides*, are the dominant forms. It is proposed that the boundary in the North American standard Cambrian section be corrected in order to correspond to the position in the standard European section.

Correlation of the North American and Asiatic sections remains less accurate because of our scattered and incomplete knowledge of many of the Asiatic faunas. Howell (1947) offered a very tentative correlation, portions of which were subsequently adversely criticized by Kobayashi. There is general agreement that the faunal zones of the Fengshanian stage of the Asiatic section are the equivalents of the North American *Ptychaspis-Prosaukia* and *Saukia* zones. To date there is no known Asiatic faunal assemblage which shows a relationship with the *Conaspis* zone. It is possible that there was a break in sedimentation throughout eastern Asia, as suggested by Howell's 1947 chart. However, the distinctive American faunas of this zone are exceptionally provincial in character and could have been prevented by biofacies or land barriers from reaching the Asiatic region. The faunas of the Daizanian may have lived on through this time in Asia. The re-



TEXT-FIG. 1—Correlation of North American, northwest European and northeast Asiatic Upper Cambrian and late Middle Cambrian faunizones.

cord of *Kaolishania pustulosa*, a characteristic form of the Daizanian, associated with faunas in the lower part of the Fengshanian (Endo, 1937, p. 304), suggests that there was not an appreciably long time lapse between the two stages.

The presence of several apparently related genera suggests the equivalence of some of the Daizanian with the *Elvinia* zone. The Asiatic faunas of this stage are characterized by the genera of the Kaolishanidae. In Manchuria, where the stage was proposed by Endo (1937), several species of *Mansuyia* are associated with *Maladioidella*, *Pseudagnostus cyclopygeformis* Sun, an agnostid closely allied to the European *Pseudagnostus cyclopyge* Tullberg, and *Mansuyella tokunagai* (Kobayashi) which is a Ceratopygidae close to *Proceratopyge*. In this assemblage the suggested affinities with species in the lower zones of the Upper Cambrian of Sweden is considered significant. In North China Sun (1935) named the same faunal assemblage the *Kaolishania pustulosa* zone, which at that time was placed in the top of the Changshanian stage. The assemblage is characterized by three genera of the Kaolishanidae, *Pseudagnostus cyclopygeformis* and also a species identified as *P. cyclopyge* Tullberg, and *"Elkia" orientalis* which may be a genus of the Dokimocephalidae. There seems little doubt that these faunas are the approximate correlatives of at least zones 2 and 3 of the Scandinavian sections, and of the *Elvinia* fauna of North America.

The assemblage of the underlying zone 2 (the *Changshania conica* zone of Sun) is very different. This fauna is characterized by species of *Changshania*, *Dikelocephalites*, and species of *Agnostus*, *A. holi*, and *A.* cf. *A. pisiformis*. There is no indication of this assemblage in the south Manchuria section, but we cannot now say whether this indicates a short stratigraphic break or insufficient knowledge of the section. In the Scandinavian section *Agnostus pisiformis* (Linnaeus) ranges from the *Leiopyge laevigata* zone through zone 2, the *Olenus* zone, with maximum development in zone 1, the *A. pisiformis* zone. Thus, the *Changshania conica* zone of Asia cannot be older than the

Leiopyge laevigata zone and is most probably the correlative of zone 1.

Zone 1 (the basal zone of the Changshanian) is characterized by species of *Chuangia*. Endo records two zones from the Paishan formation: the *C. transversalis* and the *C. batia* zones, separated by 2.8 m. The assemblages are essentially the same in both zones, and contain, besides *Chuangia*, a species of *Maladioidella*, *Maladioides* (the oldest genus of the Elviniidae), *Mansuyella* sp., *Pseudagnostus cyclopygeformis* and *Agnostus hoiformis*, recorded from the overlying zones of the Daizanian. Kobayashi (personal communciation, August 12, 1955) informs me that "*Proceratopyge* is found in the *Chuangia* zone of south Manchuria," but I do not know whether this statement means the discovery of new material or is a corrected identification of Endo's specimens called *Mansuyella* sp. In North China Sun records one zone of *C. batia* which contains both species as well as several others. He finds no genera in common with his overlying *Changshania conica* zone. It is from the *Chuangia* assemblages in both Manchuria and north China that smooth trilobites identified as *Kingstonia* and generalized cranidia referred to *Crepicephalus* are reported. Otherwise the assemblages are entirely Asiatic in composition. The most significant genera appear to be *Proceratopyge*, which is widespread in central Asia also, and the agnostids. In the Scandinavian sections *Proceratopyge* ranges from the base of the *Leiopyge laevigata* zone through zone 3 of the *Olenus* beds. Thus the *Chuangia* zones of Asia appear to be the approximate time equivalents of the *Leiopyge laevigata* zone, although it is not improbable that the base of the Asiatic section may be slightly older. With this correlation the presence of *Kingstonia* and *Crepicephalus* becomes more meaningful. The species may actually belong to the same North American stocks and having found temporary refuge in the northeastern Asiatic seaways as and after the biofacies of the North American seas became unfavorable to them. However, the refuge was not too satisfactory as only two genera of the large *Cedaria-Crepicephalus* assemblage survived, and was most temporary as they also disappeared along with *Chuangia* in a relatively short time.

CORRECTIONS AND ADDITIONS

Endoaspis, new name

Endoaspis is proposed to replace *Wutingia* Endo, 1935 (genotype: *Wutingia rectangulosa* Endo from Lower Ordovician of Manchuria), Sci, Report Tohoku Imperial Univ. (2nd ser.), vol. 16, no. 4, p. 217—homonym of *Wutingia* Melichar, 1926.

Mareda, Kobayashi

Prosaukia? anomala Ulrich & Resser, 1933 is a species of the genus *Mareda* Kobayashi, 1942. The genus is a rare but distinctive member of the Franconian (*Prosaukia* subzone) of Wisconsin and the Fengshanian of northern China. *Mareda* is valuable in affording supporting evidence of the essential contemporaneity on both sides of the Pacific of the faunas characterized by genera of the Ptychaspidae and Saukiidae. *Hamashania pulchra* Kobayashi, 1942, based on a single fragmentary pygidium from the Fengshanian of Manchuria, may actually represent another species of *Mareda*. It is the only form presently known from the Cambrian faunas whose structure suggests a relationship with *Mareda*.

Strigigenalis Whittington & Ross

Strigigenalis Whittington & Ross, 1953, belongs in the recently erected family Lecanopygidae Lochman, 1953, rather than the Leiostegiidae.

Iranaspidinae, new subfamily

A new subfamily, the Iranaspidinae (of the Leiostegiidae Bradley, 1925) is proposed for the reception of two Asiatic genera, *Iranaspis* King, 1937 (genotype: *I. harrisoni* King), from the late Upper Cambrian of Persia, and *Plethopeltella* Kobayashi, 1943 (genotype: *Plethopeltis resseri* Kobayashi, 1933), from the basal Ordovician Wanwanian formation of southern Manchuria. The Iranaspidinae are characterized by:

Cranidium rectangular, glabella low, broadly rectangular, front rounded, all furrows faint, preglabellar field narrow or absent, palpebral lobe medium size, slightly posterior to center of glabella; pygidium semicircular, axis low, narrower than pleural fields, tapered 4/5 length, all furrows obso-

lete on exterior, faint on interior, narrow border, no marginal spines.

Chakasskia Poletayeva and *Inouyina* Poletayeva

The two Siberian genera, *Chakasskia* Poletayeva, 1936 (genotype: *C. minussensis*), and *Inouyina* Poletayeva, 1936 (genotype: *I. quadratica*), in basal Middle Cambrian beds, are known from only a few cranidia each and have been placed in Incertae Sedis. The work of Poletayeva (1936) and of Lermontova (1940) suggests that in the Siberian Cambrian sections some trilobite genera and families which appear in the uppermost Lower Cambrian zone may continue into the fauna of the basal Middle Cambrian zone, a situation comparable to that reported by Rasetti (1951) in the Cambrian sections of the Canadian Rocky Mountains. The structure of the cranidia of *Chakasskia* indicates a relationship with the Protolenidae and suggests that it might well be a late member of that family. Similarly it is suggested that *Inouyina* may be a specialized end member of the Antatlasiidae. Both families are very abundant in the latest Lower Cambrian and have recently been studied by Hupé (1953a). The newly established Antatlasiidae are not yet well known outside the Mediterranean region; but the Protolenidae appear to have had a world wide distribution in the northern hemisphere.

DISCUSSION OF FAMILIES

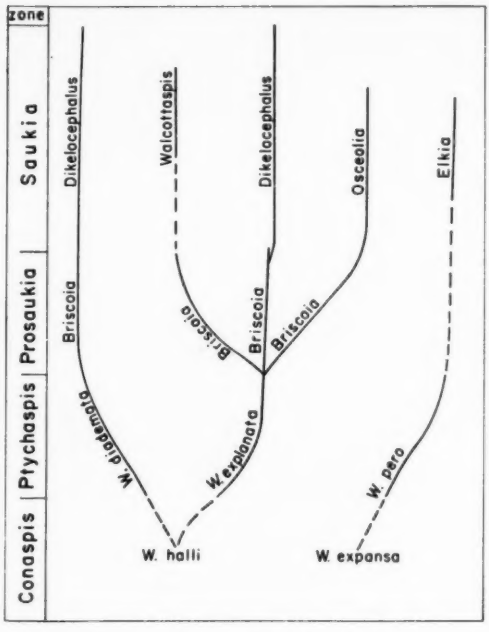
Dikelocephalidae

In 1889 Miller established the Dikelocephalidae based on *Dikelocephalus* of the late Upper Cambrian beds of Wisconsin. During the ensuing years the family had become a general catchall by the constant addition of related and unrelated Upper Cambrian and Lower Ordovician genera. Kobayashi (1933, 1935) traced the history of the family and recognized six subfamilies: Dikelocephalinae, Osceolinae, Saukiinae, Ptychaspidinae, Hungaiinae, ?Richardsonellinae. To these he added the Dikelokephalininae in 1936. Hupé (1953) recognized most of these as independent families, in some instances not closely related. More complete information available to me on these families has necessitated additional corrections for the Treatise.

The Dikelocephalidae Miller, 1889, (s.s.), contains the genera *Briscoia* Walcott, 1925, *Dikelocephalus* Owen, 1852, *Elkia* Walcott, 1925 (synonym *Parabriscoia* Kobayashi, 1935), *Osceolia* Walcott, 1914, and *Walcottaspis* Ulrich & Resser, 1930; and its stratigraphic range is from the base of the *Prosaukia* subzone of the Franconian to the top of the *Saukia* zone of the Trempealeauan. The rise of the family in the North American seaways by the evolution of *Briscoia* from the early Franconian genus *Wilbernia* can be demonstrated in the numerous collections of the upper Mississippian Valley (Raasch, 1952). One of the early transitional species of *Briscoia*, *B. pertransversa*, n. sp., is described in this paper (see below). *Briscoia* was the most plastic genetically and the most adaptable. It alone migrated through the boreal seaways into northwestern Europe and northeastern Asia. The species of the other four genera apparently were developed polyphyletically from the numerous early species of *Briscoia*. They were all restricted to North America.

In the late 1930's Dr. Josiah Bridge obtained a number of collections from the lower "Pogonip" limestone of the Eureka district, Nevada. In this material the cranidia of *Elkia nasuta* Walcott occur always associated with the pygidia of *Parabriscoia dolichorachis* Kobayashi. Several collections are a trilobite coquina composed entirely of these cranidia and pygidia and specimens of *Pseudagnostus*. Several of these specimens of *Elkia nasuta* and *Parabriscoia dolichorachis* are figured (Pl. 47, fig. 5–14). *Parabriscoia* was founded on the pygidia of *P. elegans* Kobayashi (1935a) from Alaska, which is clearly congeneric with *P. dolichorachis* from Nevada, and consequently the genus becomes a junior subjective synonym of *Elkia*.

The division of the genera of Dikelocephalidae into two subfamilies, the Dikelocephalinae and the Osceolinae, made by Ulrich & Resser, (1930), is unnecessary and unnatural and is not recognized. The major irreversible trends in the evolution of the Dikelocephalidae (Text-fig. 2) appear to have been 1) a gradual increase in length of eye and palpebral lobe, 2) the consequent narrowing (exsag.) of the posterior limb, 3)



TEXT-FIG. 2—Evolution of the Dikelocephalidae.

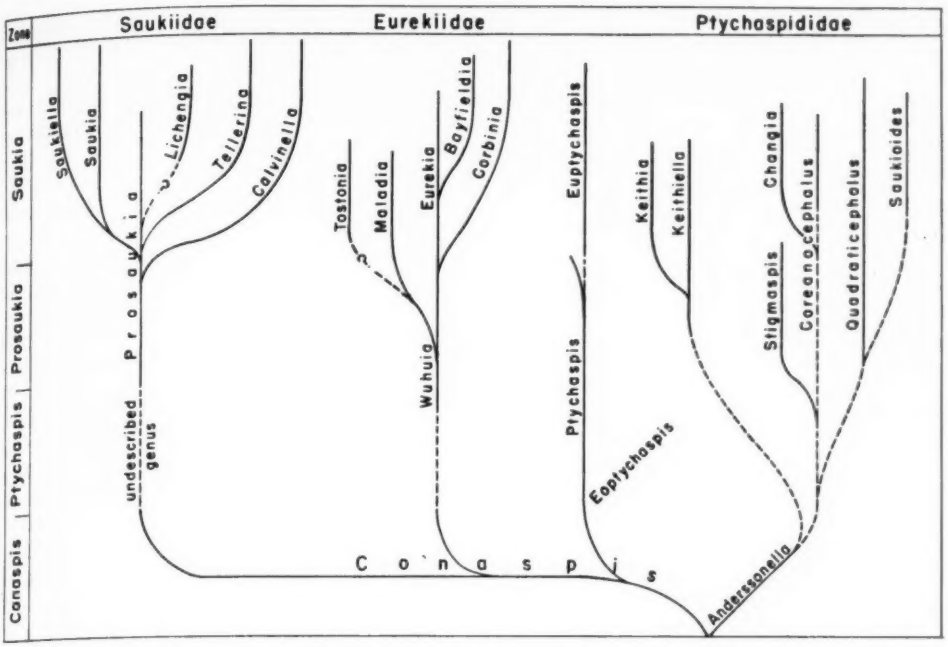
the widening of the border of the pygidium with the sporadic adoption of marginal spines which do not seem to have been too satisfactory, 4) a broadening and squaring of the front of the glabella, and 5) a modification of the frontal area and frequent obsolescence of the anterior border furrow.

Ptychaspididae, Saukiidae and Eurekiidae

The Ptychaspididae Raymond, 1924, the Saukiidae Ulrich & Resser, 1930, and the Eurekiidae Hupé, 1953, comprise three groups of genera which trace their ancestry from the extremely plastic early Franconian genus *Conaspis*. Consequently, they are essentially unrelated to the Dikelocephalidae except that both ancestral genera were originally derived from Middle Cambrian ptychopariid stock. *Conaspis* appeared in the North American seaways about the middle of *Conaspis* zone time and moved southeastward along the western shore of Laurentia into the Mississippi Valley region and on into the central Appalachians. Although the genus has become better known in recent years through the work of Nelson (1951), Wilson (1951), Bell, Feniak & Kurtz (1952) and Berg (1953), the published illustrations still give only a faint idea of the infinite variety of small detail which can be observed in the several hundred specimens of *Conaspis perseus* at the University of Minnesota.

Nelson's material revealed the unquestioned descent of *Eoptychaspis* and *Ptychaspis* from *Conaspis*. In 1953 Lochman discussed the Ptychaspididae briefly. Recent work has added three more Asiatic genera (*Changia* Sun, 1924, *Saukioides* Kobayashi, 1952, and *Coreanocephalus* Kobayashi, 1935) which apparently belong to the line of descent from *Anderssonella* (Text-fig. 3). A fourth genus, *Wuhuia* Kobayashi, 1933, appears in Asia in the early Fengshanian faunas associated with the other genera of the Ptychaspididae and with the Saukiidae. Although I have recognized *Wuhuia* for the present as a separate genus, it is actually very similar to *Conaspis*. It is quite possible that *Wuhuia belus* (Walcott) is really only a late *Conaspis* species which migrated with the members of the *Ptychaspis-Prosaukia* faunal assemblage from the northern Cordilleran seaways into northeast Asia at the beginning of the Fengshanian stage. But a final conclusion must await the description of the Franconian faunas of northwestern Canada. The Ptychaspididae reached the height of their genetic diversification and geographic distribution at the end of the Franconian and early part of the Trempealeauan, and then gradually dwindled in importance during the later Trempealeauan.

The *Conaspis-Wuhuia* stock is believed to have given rise to the small late Upper Cambrian family, the Eurekiidae. Five genera (*Eurekia* Walcott, 1925, *Bayfieldia* Clark, 1924, *Corbinia* Walcott, 1925, *Maladia* Walcott, 1925, and *Tostonia* Walcott, 1924) are placed in the family. Of these, *Maladia*, associated with late *Prosaukia* zone faunas in the Cordilleran region, appears to be the earliest and is also the least specialized form. In *Maladia* the pygidium has already acquired 5 pairs of the characteristic short marginal spines, but the cranidium still has an eye ridge present, a triangular posterior limb, a wider palpebral area and the palpebral lobe near the center of the glabella. The other, more specialized genera are known only from *Saukia* zone faunas.



TEXT-FIG. 3—Descent of the Saukiidae, Eurekiidae and Ptychaspididae from *Conaspis*.

The boreal seas of the northern Cordilleran region are regarded as the probable home of the family. It is best known and most abundantly represented in the Cordilleran and upper Mississippian Valley regions of the United States. Only *Bayfieldia* occurs in the late Upper Cambrian faunas of the St. Lawrence region.

The Saukiidae are also believed to be derived from *Conaspis*. Six genera (*Saukia* Walcott, 1914, *Calvinella* Walcott, 1914, *Lichengia* Kobayashi, 1942, *Prosaukia* Ulrich & Resser, 1933, *Saukiella* Ulrich & Resser, 1933, and *Tellerina* Ulrich & Resser, 1933) comprise the family. Of these *Prosaukia* is clearly the most primitive in structure and much the earliest in time of appearance. Ulrich & Resser (1930, p. 13; 1933, p. 135) mention an undescribed genus, *Saukaspis*, which is regarded by them as bridging the gap between *Ptychaspis* and *Saukia*, and presumably implying, since *Ptychaspis* is much earlier in time, that it was the ancestral form. But on p. 14 they state

> These suggested reversions to ancestral characters are not to be understood as implying our belief that *Saukia*, *Tellerina*, and *Calvinella* were evolved out of known Franconia or Mazomanie species of *Prosaukia*. What we do believe is that all four of these generic types had a common pre-Franconia ancestor whose characters are more nearly reproduced in *Prosaukia* than in the others.

The authors make no effort to reconcile their two statements. Raasch (1952, p. 149) presents a third opinion, indicating in his *Ptychaspis* subzone "*Ptychaspis*, ancestral to *Prosaukia*." All efforts to find any material, labeled or unlabeled, which might represent the undescribed genus, *Saukaspis*, have failed to date, and I am unable to determine what form Ulrich and Resser may have had in mind. In view of the fully documented evolutionary trends established for the *Conaspis*→*Eoptychaspis*→*Ptychaspis* series, it does not appear probable that a typical species of *Ptychaspis* would have undergone such a complete reversal of all dominant trends as to produce a primitive *Prosaukia* species. I postulate that the line of descent of the Saukiidae began with one of the variants of *Conaspis perseus*, and that this form should be looked for among the faunas of the *Ptychaspis* subzone. In the holotype cranidium of *Conaspis perseus* (Berg, 1953, pl. 60, fig. 5) the glabella is

more elongate rectangular than usual, the palpebral lobes arcuate, slightly longer than those in Berg's fig. 7 and just slightly posterior to the center of the glabella. The posterior pair of glabellar furrows may be complete or broken. In such a cranidium as Berg's fig. 5 an increase in size and further posterior movement of the palpebral lobes would make it hard to distinguish from *Prosaukia* except for the slightly more conical glabella. Then broadening of the front of the glabella would produce a typical *Prosaukia*. In the pygidium, also, an increase in size which would elongate the axis and widen the border is all that is needed to change the small semicircular pygidium of *Conaspis* into a typical *Prosaukia* pygidium.

During the past several decades there has been disagreement as to the genotype species of *Saukia* Walcott, 1914. Walcott designated *Dikellocephalus lodensis* Whitfield, 1880, but added immediately after the name "(pl. 65, fig. 1)" referring to his figure of the plaster cast, USNM 58618, of a complete *Saukia* exoskeleton (Walcott, 1914, p. 374). The original from the Edgar E. Teller collection is now at the U.S. National Museum and bears the same number. It was collected at USNM locality 85, Prairie du Sac, Sauk County, Wisconsin. The species of *Dikellocephalus lodensis* was described from several specimens of a pustulose free cheek collected from the "Mendota" beds at Lodi, Wisconsin. The holotype specimen (Whitfield, 1882, pl. 10, fig. 14) is now Univ. of California 1219/34342 (Peck & McFarland, 1954). Such a free cheek is actually specifically unidentifiable, and *Dikellocephalus lodensis* was thus an unrecognizable species; a fact of which Walcott was apparently well aware when he attempted to substitute the complete specimen from Prairie du Sac. Later in the same publication Whitfield (1882, p. 341, pl. 27) describes and figures a separate cranidium (fig. 13) and an exoskeleton of one free cheek, thorax and pygidium (fig. 12), from Prairie du Sac. The cranidium, Univ. of California 1219/34341, belongs to *Tellerina crassimarginata* (Whitfield) which also occurs abundantly at this horizon and locality; but the incomplete exoskeleton does belong to some species of *Saukia*. In 1914 Walcott's topotype material, the complete exoskeleton USNM 58618, revealed the characteristics of this species; but it does not follow, as Walcott assumed, that the Prairie du Sac species is the same as that found at Lodi. Consequently, in 1914 *Dikellocephalus lodensis* was still an unrecognizable species. Strangely enough, no special effort was made then or has been made subsequently to obtain adequate topotype material of *Saukia* from Lodi, Columbia County, Wisconsin.

In 1933 Ulrich & Resser had topotype material of *Saukia* from Lodi consisting of two cranidia and some free cheeks. They called the cranidia a new species, *Saukia ornata*, holotype MPM (Milwaukee Public Museum) 19387. In view of the fact that the cranidia show the same densely granular surface so characteristic of the free cheek of *Dikellocephalus lodensis* it would have been more reasonable to have considered it as the associated cranidium of that species [in 1952 Raasch did assign them to *Saukia lodensis* (Whitfield)]. Instead Ulrich & Resser designated a very imperfect cranidium, MPM 19397, from 2 miles south of Spring Green, Sauk County, Wisconsin, as the plesiotype of *Saukia lodensis*. This assignment was an entirely arbitary guess since the cranidium was not associated with any other trilobite parts which had ever been assigned to *Dikellocephalus lodensis*. Nevertheless, Ulrich & Resser in 1933 accepted *Saukia lodensis* (Whitfield) as a valid species, and recognized specific differences between the holotype free cheek of *S. lodensis* and the free cheek of the complete *Saukia* exoskeleton figured by Walcott in 1914. On the basis of these distinctions, USNM 58618 from Prairie du Sac was made the holotype of a new species, *Saukia acuta*, by them. Ulrich & Resser then argue that, although Walcott designated *Dikellocephalus lodensis* Whitfield, 1880, as the genotype, the fact that he cites after the name the picture of the complete exoskeleton, USNM 58618, indicated that Walcott had in mind that one specimen as the genotype, and consequently the genotpye species now became the new species of *Saukia acuta* Ulrich & Resser. Obviously, this argument is nomenclaturally invalid, especially since Ulrich & Resser had claimed *Saukia lodensis* (Whitfield) as a valid and recognizable species, an opinion which was still open to question after their work.

In order that *Dikellocephalus lodensis*

Whitfield, 1880, may be accepted without question as a recognizable species, I propose that the cranidium, MPM 19387, from Lodi, Wisconsin, the holotype of *S. ornata* Ulrich & Resser, be established as a plesiotype cranidium of *Saukia lodensis*. I urge that every effort be made to obtain additional topotype material from USMN, locality 86 so that the species may be better known. The cranidium of *S. lodensis* (Whitfield) is characterized by: 1) the subdued profile and negligible expansion of the anterior lobe of the glabella (the sides of the glabella may even seem to converge slightly forward); 2) the straight or very slightly curved anterior border furrow lying tangent to the preglabellar furrow at the midline of the glabella, leaving tiny triangles of the preglabellar field at the sides; and 3) the second pair of glabellar furrows may be nearly complete. The species is distinct from *S. acuta* Ulrich & Resser from Prairie du Sac, the cranidium of which is characterized by: 1) an expanded anterior lobe of the glabella (the sides of the glabella diverge anteriorly and the front of the glabella has pushed forward so that the convex anterior border appears to curve around it); 2) the anterior border furrow is distinct only in front of the fixed cheeks and runs diagonally backward to the anterolateral corners of the glabella. It should be mentioned that the densely granular surface is a generic, not a specific characteristic.

Hungaiidae, Remopleurididae and Ptychopariidae

The remaining families are wholly unrelated stocks. *Hungaia*, from the St. Lawrence and Cordilleran seaways of Canada, is the sole genus of the Hungaiidae, and its relationship is uncertain. The structure of both cranidium and pygidium is unlike that of any of the late Upper Cambrian genera with which it has frequently been compared, but the pygidium does show many features commonly observed in basal Ordovician (Tremadoc) genera, such as *Kainella* of the Remopleurididae. *Hungaia* may be an early aberrant offshoot from that stock.

Richardsonella has subsequently been placed in the Remopleurididae and the other genera included in the Richardsonellidae by Kobayashi (1935) have all been reassigned to other families.

Conokephalina of the late Middle Cambrian and early Upper Cambrian of Europe has been regarded as a possible ancestor of the Dikelocephalidae (Walcott, 1914) and of the Ptychaspidoidae (Hupé, 1953). The genus had also been erroneously identified in many Upper Cambrian Asiatic and North American faunas. However, now the old errors of generic identification have been corrected, and the immediate ancestral genera of the Dikelocephalidae, Ptychaspididae and Saukiidae have been recognized. Actually *Conokephalina* and the related *Lobocephalina* are quite close to *Ptychoparia* with which species of both genera are associated. The narrower fixed cheek and very weak eye ridge are features of specialization in the cranidium, and the narrow transverse shape of the pygidium is not uncommon in the Ptychopariidae. The two genera have been placed as a separate subfamily (the Conokephalininae Walcott, 1913) under the Ptychopariidae. The two genera are so similar in appearance that it may be found, when more better preserved material has been collected, that they are really only geographic variants of the same genus: *Conokephalina* in northern Europe and *Lobocephalina* in Bohemia.

Dikelokephalinidae

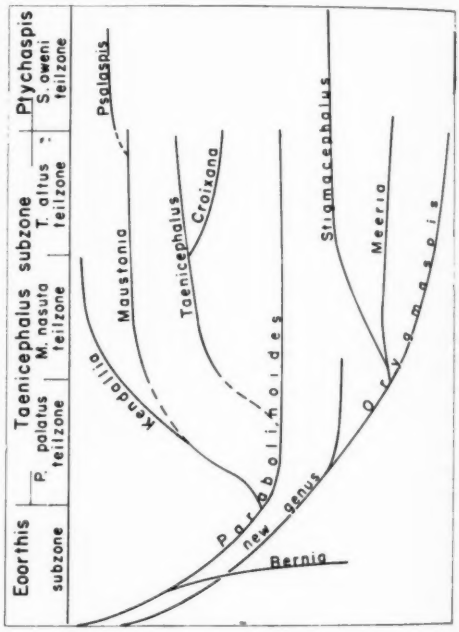
The Dikelokephalinidae Kobayashi, 1936, is a separate family in no way related to the Dikelocephalidae or any of the other preceding families. All the genera occur in the early Lower Ordovician and are distributed from northwest Europe through central Europe and Asia to far eastern Asia and Tasmania, but are not known in the western hemisphere. I believe that these genera represent a very primitive and short-lived branch of the basic stock which gave rise to the dominant Asaphoidae of the Lower and Middle Ordovician (Text-fig. 5). It must be assumed that the stock evolved from one of the generalized ptychopariid genera living in the latest Middle Cambrian. Comparison with another primitive member of the stock, *Eoasaphus*, in zone 3 of the Upper Cambrian of Sweden, is helpful. In this genus the semicircular pygidium is medium sized, with only four axial rings and terminal. The cranidium is more advanced in that the fixed cheeks are already narrow, but a primitive conical glabella with short

diagonal glabellar furrows, medium sized palpebral lobes centrally placed and a shallow anterior border furrow are still present. An enlarging of the pygidium and minor changes in the cranidium lead readily to *Nileus*. By contrast the genera of the Dikelokephalinidae combine an advanced enlarged pygidium with a basically primitive cranidium. The glabella remains conical, the fixed cheeks of medium width, the palpebral lobes medium sized to large, the eye ridge prominent and the frontal area unrestricted. The loss of the anterior border furrow, the development of the posterior pair of alae, the posterior position of the palpebral lobes, and the peculiar pit-like glabellar furrows constitute the only specializations in the cranidium. The paired marginal spines of the pygidium are insignificant homoeomorphic features. Such spines, similar in appearance but different in structure, appear again and again on the pygidia of unrelated stocks from the late Middle Cambrian, through the Upper Cambrian and the Lower Ordovician. A ready example is a comparison of the spines of *Hungioides novaki*, produced by broad serrations of the border, with the similar appearing spines of *Hungaia* which are the spined ends of the ankylosed pleurae of the pygidium. The Dikelokephalinidae was an unprogressive and aberrant branch which gave rise to no later descendant. Its widespread geographic distribution in the Eurasian seaways is indicative of its ancient lineage and supports its primitive position on the line of descent of the basic Asaphoidae stock.

Parabolinoididae, new family

In the *Conaspis* zone of the Franconian of North America there occurs a group of related genera which have until recently been very poorly known. A new family, the Parabolinoididae, is proposed, from the name of one of the early genera. The family contains *Parabolinoides* Frederickson, 1949, *Bernia* Frederickson, 1949, *Croixana* Nelson, 1951, *Kendallia*, Berg, 1953, *Maustonia* Berg, 1953, *Meeria* Frederickson, 1949, *Orygmaspis* Resser, 1936, *Psalaspis* Resser, 1937, *Stigmacephalus* Resser, 1936, *Taenicephalus* Ulrich & Resser, 1924, and a new genus being described by J. L. Wilson to include *"Parabolinella" evansi* Kobayashi and *"Parabolinella" occidentalis* Wilson. The family ranges from the *Aphelaspis* zone, in which the new genus first makes its appearance, through the *Conaspis* zone, when the family is at its height, into and through the lower half of the *Ptychaspis* subzone (Text-fig. 4).

The Parabolinoididae are characterized by: Opisthoparian subisopygous exoskeleton; glabella conical to truncato-conical, three pairs of glabellar furrows distinct to obsolete, eye ridge distinct to faint, palpebral furrow distinct to obsolete, frontal area one-third to one-fourth length of cranidium, anterior border furrow distinct to obsolete, eye just under medium size to small, fixed cheek one-half to one-third and less glabellar width, posterior area triangular to strap-like; free cheek rectangular with genal spine; pygidium transverse to subtriangular, axis convex, tapered nearly full length to broadly rounded end, three to four axial rings and four pleurae, interpleural grooves and pleural furrows distinct to obsolete, border furrow faint to obsolete, poorly defined border, one to four pairs of marginal spines



TEXT-FIG. 4—Evolution of the Parabolinoididae.

or margin smooth. Outer surface smooth or finely granular.

Two lines of descent are recognized within the Parabolinoididae, one with *Parabolinoides* as the most primitive genus, the other with Wilson's new genus. In the two genera most features of the exoskeleton are very similar, the size and position of the eyes and palpebral lobes being the major distinction between them. Both genera strikingly resemble genera of the Olenidae (*Olenus* and *Parabolina* especially, as the name *Parabolinoides* implies). The earliest species of the new genus is associated with *Aphelaspis* in the Marathon uplift of Texas (Wilson, 1954) and is the earliest olenid-type trilobite known. It is not improbable that it may be the ancestral genus of both families. During the succeeding *Elvinia* zone time *Olenus* developed as a separate genus and established the independently evolving Olenidae, in the Scandinavian seaways. And *Parabolinoides* developed in the western hemisphere to give rise to a second branch of the Parabolinoididae. With the second major biofacies change at the beginning of *Conaspis* zone, both genera appear in the North American faunal assemblages.

Wilson's new genus is characterized by a conical glabella, three pairs of distinct glabellar furrows, eye almost medium sized, near center of glabella, a wide (tr.) well-developed frontal area with distinct anterior border furrow, fixed cheek one-half to one-third glabellar width, and a medium-width (exsag.) triangular posterior area; a transverse pygidium with one to three pairs of marginal spines. Within the genus an important evolutionary trend of the whole family can be detected by comparing "*P.*" *evansi* with the later "*P.*" *occidentalis*. The fixed cheeks have become noticeably narrower, and the palpebral lobes have moved slightly forward.

Parabolinoides is characterized by a conical glabella, three pairs of distinct glabellar furrows, eye small and opposite anterior third of glabella, a wide (tr.) well-developed frontal area with distinct anterior border furrow, fixed cheek one-third glabellar width, and a broadly triangular posterior area along which the posterior course of the facial suture runs in a diagonal course directly from the base of the palpebral lobe; a narrow transverse pygidium with one to four pairs of marginal spines. *Parabolinoides* dominated the *Eoorthis* subzone and during this time gave rise only to the very similar, short-lived *Bernia*.

In the succeeding *Taenicephalus* subzone both stocks give rise to a number of genera. The two stocks show a striking parallelism in their development as the dominant trends are the same in each branch but appear in each at a different rate. The dominant trends are: 1) glabella becomes truncato-conical, 2) furrows on cephalon become faint and obsolete, especially the glabellar furrows and the anterior border furrow, 3) the facial suture moves inward—the frontal area and fixed cheek become much narrower, and the posterior branch of the facial suture tends to run backward at first from the end of the palpebral lobe until ultimately its course is a distinctive sigmoidal curve, and 4) the posterior margin of the pygidium becomes smooth.

The parallelism had made it difficult to unravel the relationships until Berg (1953, p. 556) worked out the stratigraphic ranges of the genera and species in the *Conaspis* zone. In line I (*Kendallia*→*Maustonia*→*Psalaspis*) all the trends are much accelerated, and even the axial furrow becomes quite faint. This group might be considered the most progressive branch. In line II (*Taenicephalus*→*Croixana*) several of the trends are decelerated, the obsolescence of the anterior border furrow appearing only in the late, short-lived *Croixana*. In line III (new genus—*Orygmaspis*→*Meeria*→*Stigmacephalus*) all the trends develop at a steady and moderate rate.

The biofacies of the *Conaspis* zone is distinctive and widespread throughout the United States, but the strata of the zone are usually not thick. The family does seem to be most completely represented in the formations in the Mississippi Valley region. It is probable that the North American interior seaway was the indigenous site of its evolution. In the sandstones of the upper Mississippi Valley specimens of the Parabolinoididae are extremely abundant and the genera and species are as yet best known from this region (Nelson, 1951; Bell, Feniak & Kurtz, 1952; Berg, 1953). The fauna has also been described from Oklahoma (Frede-

rickson, 1951) and is being described from Texas (Ellinwood). The *Parabolinoides* stock appears to have moved southeastward along the western coastal shelf of Laurentia to reach the interior of the United States. The new genus branch of the family may have followed a similar route or may have penetrated the interior from a southern seaway.

These genera were two of a group of migrants whose appearance in the North American seaways about the beginning of *Conaspis* zone time seems to have been favored by a biofacies change occurring in the interior seaways at this time. This change caused the eventual extinction of many of the characteristic genera and species of the *Elvinia* zone, although there is definite evidence in the Mississippi Valley region of the temporary cohabitation of the new migrants with the old stocks. As the old genera died out, ecologic niches were left available to the descendants of the new migrants. After dominating the trilobite fauna during the *Conaspis* zone, the Parabolinoididae dwindled rapidly at the beginning of the *Ptychaspis* subzone. Two specialized genera, *Psalaspis* and *Stigmacephalus*, held out for a time in restricted localities against the descendants of *Conaspis;* then the family became extinct.

Conaspis had appeared and maintained itself among the Parabolinoididae during the entire upper half of the *Conaspis* zone; but it was not until the *Stigmacephalus oweni* teilzone (the time recognized as the base of the *Ptychaspis* subzone) that its variants succeeded in establishing independent genera. This fact combined with the rapid dwindling and extinction of the Parabolinoididae indicates that another major biofacies change was occurring in the North American seaways at this time. The evolutionary continuity of the American faunas of the *Ptychaspis-Prosaukia* and the *Saukia* zones suggests that no other major change in biofacies occurred during the rest of the Upper Cambrian.

The three times of relatively sudden biofacies change in the North American seaways (1) at the beginning of *Aphelaspis* zone time, 2) at the begining of *Conaspis* zone time, and 3) at the beginning of *Ptychaspis* subzone time) were primarily responsible for the marked changes in faunal composition which distinguish the North American faunizones. With each biofacies change the earlier indigenous dominant trilobite genera waned and died, leaving room for the expansion of unrelated migrant stock. This situation is in striking contrast to the faunizones of the Scandinavian Upper Cambrian where the stability of a single environment permitted continuity of development of a single dominant stock, the Olenidae.

Shirakiella Kobayashi

Kobayashi (1935) described the genus *Shirakiella* (very similar in appearance to *Kendallia*) from the *Kaolishania* zone of Korea, genotype: *S. elongata* Kobayashi of which only the cephalon is known. At the same time Kobayashi described an additional species, *S. laticonvexa*, from one of the cranidia referred to *Coosia tokunagai* Kobayashi. However, the holotype cranidium of this species (Kobayashi, 1935, pl. VII, fig. 15—error gives fig. 16, a free cheek) is obviously conspecific with the holotype of *C. tokunagai*. In 1937 Endo figured additional cranidia and associated pygidia of the latter species which he made the genotype of his new genus *Mansuyella*, a member of the Ceratopygidae. In 1947 Sun (p. 3) lists *Shirakiella laticonvex* from strata of Fengshanian age in the Paoshan region, western Yunnan. But without illustrations it is impossible to say whether *Shirakiella* or *Mansuyella* is represented by this listing. In 1953 Hupé made the genus the type and sole member of the Shirakiellidae. In our world correlation (Text-fig. 1) the *Kaolishania* zone is approximately equivalent to the upper part of the *Elvinia* zone. Thus it would appear that *Shirakiella elongata* pre-dates both the ancestral *Parabolinoides* as well as *Kendallia;* but until the matter of correct identification can be settled, it is impossible to determine its true relationship to the American Parabolinoididae. It has been considered advisable, until more is known about *Shirakiella* and its stratigraphic range, to keep it entirely separate, since the apparent similarities could easily be nothing more than a case of homoeomorphy in entirely unrelated stocks.

Housiidae

Housia is the sole member of the Housiidae. This genus, represented by three species, is widely distributed in the North

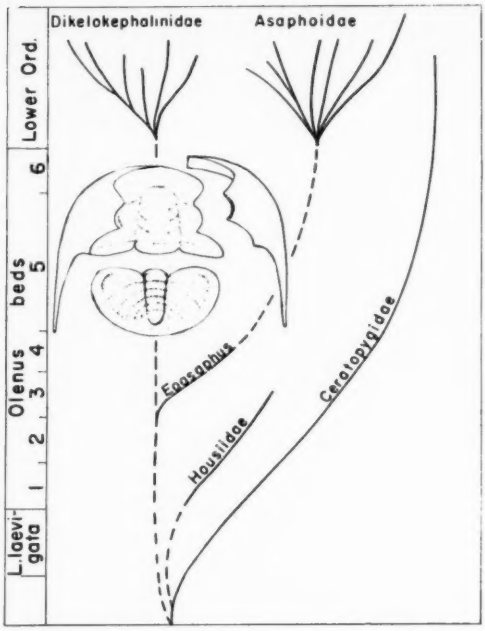
American *Elvinia* zone faunas. It appeared as one of the migrants of this fauna coming from the far northern Cordilleran or boreal seas at the beginning of the Franconian. Wilson (1951), whose specimens of *Housia vacuna* occur in limestone, noted that over half of his 150 pygidia showed the anterior segment in various stages of disarticulation, several with two anterior segments partially disarticulated, and many more in which the segment is lost. This condition suggests that the prominent anterior segment was in the process of being ankylosed to the pygidium, and that genetic instability produced either a reduction or an enlargement of the pleural ends. Wilson suggests that the cranidium with its narrow fixed cheeks, weak furrows and intramarginal course of the anterior facial suture shows a morphological relationship to the asaphids. *Eoasaphus* occurs in the Scandinavian Upper Cambrian section in zone 3, the apparent correlative of the top of the *Elvinia* zone. In the cranidium of *Eoasaphus* the fixed cheeks are wider, the palpebral lobe slightly larger and nearer the center of the glabella, the frontal area much narrower (sag.). The thoracic segments are eight in number compared to 10 in *Housia*, and the semicircular pygidium with four axial rings and terminal has all pleurae solidly fused and the margin smooth. Clearly *Eoasaphus* could not have been a direct descendant of *Housia*, but the primitive morphologic features of the asaphids, as revealed in *Eoasaphus*, do not preclude *Housia* from being an aberrant genus of that stock.

Housia has more frequently been compared with the widespread Eurasian genus, *Proceratopyge* of the Ceratopygidae, ranging from the *Leiopyge laevigata* zone through zone 3 of the *Olenus* beds, but unknown in the western hemisphere. *Proceratopyge* has eight to nine thoracic segments and a pygidium of four axial rings and terminal and the anterior spined segment solidly fused. In the cranidium the glabella retains the primitive conical shape, the palpebral lobes are flap-like, anterior in position as in *Housia* and the posterior area has the same shape and length as that of *Housia;* but the fixed cheeks are wider (one-half to one-third the glabellar width) and the frontal area is quite variable both in length (sag.) and strength of anterior border furrow. In both genera the doublures of the free cheeks are rather wide (sag.) and meet along a median suture, a feature also found in the asaphids (Rasetti, 1952).

Ceratopygidae

Kogenium from the late Middle Cambrian *Olenoides* zone of China is the earliest known Ceratopygidae. The pygidium is very similar to *Proceratopyge* with the anterior segment firmly fused. A generalized pytchopariid cranidium is doubtfully associated by Kobayashi, so no information is really available on that part of the exoskeleton. The genus does show, however, that the dominant evolutionary trends in the Ceratopygidae were already established in the late Middle Cambrian. *Housia* clearly is distinct from *Proceratopyge*, not a synonym as suggested by Whitehouse (1939). I believe that there is a relationship between the two genera, but that it is best explained as a minor parallelism in morphic features between two separate lines related through a common ancestor in the Middle Cambrian. The Ceratopygidae are a progressive accelerated branch in which the two anterior segments of the pygidium were quickly anchylosed and the thoracic segments reduced to eight relatively rapidly. *Housia* represents an unprogressive retarded branch which never did achieve either on these features and probably retained primitive features in the soft parts as well, accounting for its comparatively short life.

I think that serious consideration should be given to the fact that the Ceratopygidae, *Housia* and the asaphids all appear to have the same type of facial suture. Considering, in addition, the various features of similarity between the unprogressive *Housia* and *Eoasaphus*, I believe it quite possible that all three branches were derived from the same basic ancestral stock. Text-fig. 5 depicts the postulated lineages. The median genus of the basic stock is visualized as a trilobite with a generalized ptychopariid cranidium on which the characteristic facial suture was developing, at least 10 thoracic segments, and a medium-sized, semicircular pygidium of four to five axial segments. Unless the characteristic facial suture could be demonstrated, it would be hard to segregate such a form from many of the generalized trilobites of the late Middle Cambrian



TEXT-FIG. 5—Assumed appearance of basic stock and lines of descent of the Ceratopygidae, Housiidae, Dikelokephalinidae and Asaphoidae.

and Upper Cambrian. The various lines of descent are only recognized once the direction of the major trends has become apparent.

Coosellidae, Pterocephaliidae, and Idahoiidae, new family

During the past several decades a large group of trilobites has accumulated under the Pterocephalinae Kobayashi, 1935. *Pterocephalia* had at one time been placed in the Dikelocephalidae. Many of these genera have a broad (sag.) frontal area, and a broad pygidial border, and some may have an occipital spine. Subsequently the Middle Cambrian genera have all been removed. Recent work on Upper Cambrian faunas of Texas (Palmer, 1954) has made better known the ancestral genera of *Pterocephalia*. Three separate monophyletic families have been established for the genera: the Pterocephaliidae Kobayashi, 1935; the Coosellidae Palmer, 1954, and the Idahoiidae Lochman, new family.

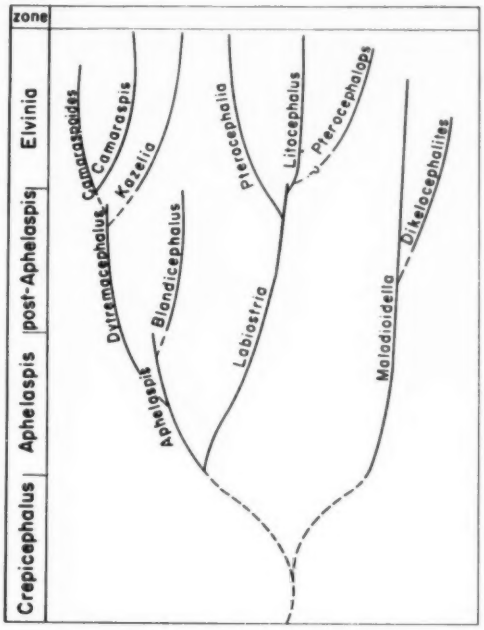
The Coosellidae contains *Coosella* Lochman, 1936, *Syspacheilus* Resser, 1938, and *Coosia* Walcott, 1911. When Palmer established the family, he also included *Crepicephalus*, a patently invalid procedure since that genus is the type of the Crepicephalidae. Palmer's argument for a close relationship between *Crepicephalus* and the other genera of the Coosellidae is based entirely upon his claim that the cranidia and pygidia of a form he has identified from the basal *Aphelaspis* zone of Texas as *Crepicephalus? perplexus* are correctly associated at the two localities where they are found and are related to *Crepicephalus*. The cranidium (Palmer, 1954, pl. 77, fig. 2) does not have the diagnostic features of a *Crepicephalus* cranidium. The elongate conical glabella, the shorter palpebral lobes and somewhat narrower fixed cheeks are similar to those of *Coosia*, and the structure of the frontal area is like *Coosella*. The pygidium is like those referred to *Coosella* and *Syspacheilus*. Granting that the cranidia and pygidia are correctly associated, I believe the species is more correctly interpreted as an aberrant *Coosia*. It certainly cannot be used to prove a close relationship between *Coosella* and *Crepicephalus*. The Coosellidae are emended to included only the three related genera of the *Cedaria-Crepicephalus* faunas of North America, and became extinct with the major biofacies change at the beginning of *Aphelaspis* zone time. The ancestors of this family should be found among either the Asaphiscidae or the pytchopariids of the late Middle Cambrian.

The Pterocephaliidae contain *Pterocephalia* Roemer, 1849, *Aphelaspis* Resser, 1933, *Blandicephalus* Palmer, 1954, *Camaraspis* Ulrich & Resser, 1934, *Camaraspoides* Frederickson, 1949, *Dikelocephalites* Sun, 1935, *Dytremacephalus* Palmer, 1954, *Kazelia* Walcott and Resser, 1924, *Labiostria* Palmer, 1954, *Litocephalus* Resser, 1937, *Maladioidella* Endo, 1937, and *Pterocephalops* Rasetti, 1944. The Camaraspididae Lochman, 1953, becomes a synonym of Pterocephaliidae. The North American genera are now well known through the work of Palmer. The earliest genera are very close to their ptychopariid ancestors and were originally placed in the Ptychopariidae by Palmer. The primitive stock was indigenous to the far northern Cordilleran seas and was able to spread southeastward into the North American interior seaways when the major

biofacies change occurred at the beginning of the *Aphelaspis* zone. This change was drastic and relatively sudden and eliminated nearly all the characteristic trilobite genera of the preceding zones. As in the case of the Parabolinoididae, we note the rapid deployment of the migrant stock into available ecologic niches. Most of these genera did not survive the isostatic and lithofacies changes which were widespread at the end of the Dresbachian, but their descendants persisted until the end of the *Elvinia* zone when the second major biofacies change occurred (Text-fig. 6). The biofacies changes were more critical in the life history of the biologically related groups than the lithofacies changes.

The lithofacies changes at the end of the Dresbachian appear to have encouraged the development of genera emphasizing one of the dominant evolutionary trends of the *Aphelaspis* stock—the development of a smooth convex cephalon by the gradual obsolescence of all the furrows. It appears that both *Dytremacephalus* and *Aphelaspis* gave rise to such genera which competed for the same or very similar ecologic niches. The descendants of the former genus were the more successful. *Blandicephalus* arose directly from such a species as *Aphelaspis longifrons*. *Dytremacephalus granulosus* of the post-*Aphelaspis* zone may be regarded as the immediate ancestor of *Camaraspoides* from which *Camaraspis* evolved by further development of the same trend. *Kazelia* appears also to have been derived from the *Dytremacephalus* stock, but an immediate ancestral species is not yet known.

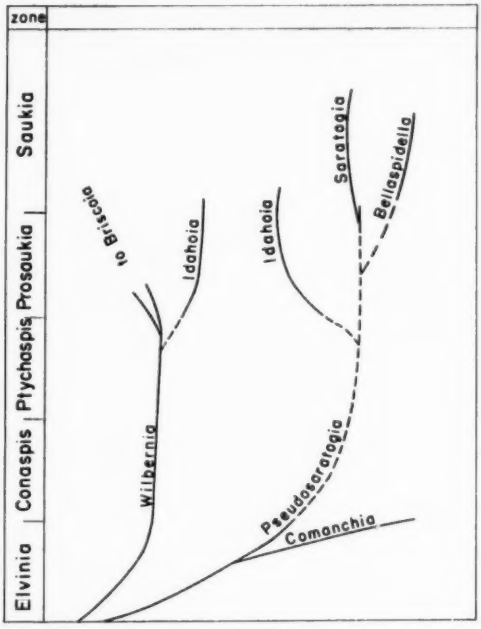
Some of the ancestral stock of the family also migrated southwestward into Asia at about this same time. The marked similarity in both cranidium and pygidium of *Maladioidella* to *Aphelaspis* I believe indicates a real biologic relationship and not simply a case of homoeomorphy. Endo records *Maladioidella* from the Daizanian associated with *Mansuyia*, *Pseudagnostus cyclopygeformis* Sun and *Mansuyella tokunagai* (Kobayashi), and from the preceding *Chuangia transversalis* zone (Text-fig. 1). In structure *Maladioidella* seems about as primitive as *Aphelaspis*. By contrast, *Dikelocephalites flabelliformis* Sun is most similar to the later, more specialized Pterocephalia, and is recorded from the *Changshania conica* zone of China. Thus it would appear to have been a contemporary of *Pterocephalia*. At present it is assumed that the American and Asiatic lineages developed separately, (Text-fig. 6) and that *Maladioidella* and *Aphelaspis* differentiated from the common ancestor just before *Aphelaspis* zone time. But when the faunas of the Canadian Cordilleran seaways are known, it may be found that there was continued movement of genera of this family between the two regions.



TEXT-FIG. 6—Evolution of the Pterocephaliidae.

The Idahoiidae contain *Idahoia* Walcott, 1925, *Bellaspidella* Rasetti, 1945, *Comanchia* Frederickson, 1950, *Pseudosaratogia* Wilson, 1951, *Saratogia* Walcott, 1916, and *Wilbernia* Walcott, 1924, and range from the base of the Franconian into the lower part of the Trempealeauan. The family is characterized by:

Opisthoparian heteropygous exoskeleton; glabella conical, truncato-conical or subrectangular, three pairs of arcuate glabellar furrows deep to faint, narrow eye ridge, broad palpebral furrow and wide palpebral rim, eye medium size or over, opposite to somewhat posterior to center of glabella, ratio of preglabellar field to anterior border very variable, occipital spine may be present, fixed



TEXT-FIG. 7—Lines of descent in the Idahoiidae.

cheek horizontal or upsloping, width variable—palpebral area arcuate, one-half to one-third glabellar width, posterior area narrow (exsag.), strap-like, medium length (tr.); free cheek quadrate, marginal furrows obsolete at genal angle, genal spine; pygidium transverse to semicircular, axis tapered to broadly rounded end with median indentation, short post-axial ridge, three to four axial rings, pleural field low, three pleurae, broad shallow pleural furrows, narrower interpleural grooves distinct to very faint, no border furrow, border of variable width; outer surface granular.

The family is an independent stock derived from a separate ptychopariid ancestor sometime during the late Dresbachian (Text-fig. 7). From the ancestral genus two genera differentiated and are believed to have maintained separate lines through the rest of the Upper Cambrian. *Wilbernia* is reported first from the *Elvinia* zone of Wisconsin and must have been in its soft anatomy a simple generalized trilobite as it proved capable of adapting to a wide variety of environments. It was one of the few genera which survived the second major biofacies change at the base of the *Conaspis* zone. The fact that it is absent from the presently known faunas of the *Eoorthis* subzone suggests that it temporarily retreated to more favorable waters at the beginning of the zone. But it appears again in the *Taenicephalus* subzone faunas and continues with considerable vigor into and through the *Ptychaspis-Prosaukia* zone (Raasch, 1952). Near the base of the *Prosaukia* subzone *Wilbernia* gave rise to several primitive species of *Briscoia*. It is possible that some of the species of *Idahoia* were also derived from *Wilbernia* since in both cranidium and pygidium it was sufficiently variable in structure to effect the necessary changes.

Pseudosaratogia, the primitive genus in the second line of descent, appeared at the very base of the Franconian and continued through the *Elvinia* zone. It gave rise to the specialized, shortlived *Comanchia* of the *Irvingella major* faunule. Both genera disappeared from the North American interior seas with the second major biofacies change. I believe that *Pseudosaratogia*, like *Wilbernia*, retreated to more favorable waters at the beginning of *Conaspis* zone time. It is suggested that this region was the far western and northern Cordilleran seas where it continued to live for some time. *Pseudosaratogia*, as a definitive genus, did not appear again, but many of the species of *Idahoia* must have developed directly out of it. The pygidium of *Pseudosaratogia* has the same body structure as *Idahoia*, but with a less expanded border; and the cranidia are very similar, only with more expanded frontal area and narrower fixed cheeks in *Idahoia*. *Idahoia* is very abundant throughout the Canadian and central Cordilleran region and apparently spread from there into the interior seas. It is believed that the poorly known Trempealeauan *Saratogia* and *Bellaspidella* may have evolved from this line also.

SYSTEMATIC PALEONTOLOGY

Family DIKELOCEPHALIDAE Miller, 1889

BRISCOIA PERTRANSVERSA, n. sp.

Pl. 47, fig. 1–4

Glabella convex, rectangular, front slightly rounded, posterior glabellar furrow complete, anterior pairs faint, narrow eye ridge, eye over medium size, opposite anterior third of glabella, frontal area just

under one-third length (sag.) of cranidium, medium-width (sag.) concave preglabellar area, narrow shallow anterior border furrow, border apparently narrow, convex, fixed cheek horizontal, narrow—palpebral area about one-third glabellar width, posterior area narrow, strap-like, length (tr.) unknown. Free cheek not known. Pygidium transverse, twice as wide as long, axis convex, tapered two-thirds length with post-axial ridge nearly to posterior margin, same width as low pleural fields, three distinct and one faint axial ring and terminal, four pleurae, pleural furrows and interpleural grooves present, only slightly curved, narrow concave border. Outer surface not preserved.

Remarks.—The material representing this species is not very well preserved and it is founded only on two pygidia and a cranidium. This is the only material now available in the Princeton Collections which could be used to illustrate one of the earliest *Briscoia* species as it developed out of *Wilbernia*. The anterior border of the cranidium is broken, but the general configuration suggests that it was moderately convex and a little narrower (sag.) than the preglabellar area. In structure of both the cranidium and pygidium there are a number of similarities to *Wilbernia explanata* (Whitfield) of the lower part of the *Ptychaspis* subzone. The pygidium differs from that of other described species of *Briscoia* in the more transverse shape, the narrowness of the concave border, and the very slight posterior curvature of the pleural furrows. In these respects the pygidium more nearly approaches that of *W. explanata*, but its generic characters are those of *Briscoia*.

Horizon and locality.—Franconia formation (*Prosaukia* zone), 1¼ miles SSE of main railroad crossing, North Freedom, Sauk County, Wisconsin.

Types.—Holotype, pygidium, PUM (Princeton University Museum) 78446; complete paratype pygidium, PUM 78447; impression of paratype pygidium; PUM 78448; broken paratype cranidium, PUM 43536.

REFERENCES

BELL, W. C., FENIAK, O. W., & KURTZ, V. E., 1952, Trilobites of the Franconia formation, southeast Minnesota: Jour. Paleont., vol. 26, p. 175–198.

BERG, ROBERT R., 1953, Franconian trilobites from Minnesota and Wisconsin: Jour. Paleont. vol. 27, p. 553–568.

ENDO, RUIJI, 1937, The Sinian and Cambrian formations and fossils of southern Manchoukuo, Part III; Addenda to Parts I and II: Manchurian Sci. Mus., Bull. 1, p. 302–369.

FREDERICKSON, E. A., 1949, Trilobite fauna of the Upper Cambrian Honey Creek formation: Jour. Paleont., vol. 23, p. 341–363.

HOWELL, B. F., 1947, Cambrian correlation between China and North America: Geol. Soc. China Bull., vol. 27 ("The Grabau Memorial Volume") p. 141–162.

—— & LOCHMAN, CHRISTINA, 1939, Succession of Late Cambrian faunas in the northern hemisphere: Jour. Paleont., vol. 13, p. 115–122.

HUPÉ, PIERRE, 1953, Classe des trilobites, *in* Piveteau: Traité de Paléontologie, vol. III, p. 44–246, Paris.

——, 1953a, Classification des trilobites: Annales de Paléont., vol. 39, p. 89–94.

KOBAYASHI, T., 1933, Upper Cambrian of the Wuhutsui Basin, Liaotung: Japanese Jour. Geol. Geog., vol. 11, no. 1–2, p. 113–130.

——, 1935, The Cambro-Ordovician formations and faunas of South Chosen, Paleontology Part III—Cambrian faunas of South Chosen: Imp. Univ. Tokyo Jour. Fac. Sci., Sect. II, vol. IV, pt. 2, p. 308–324.

——, 1935a, The Briscoia fauna of the late Upper Cambrian in Alaska with descriptions of a few Upper Cambrian trilobites from Montana and Nevada: Japanese Jour. Geol. Geog., vol. XII, no. 3–4, p. 39–57.

——, 1936, Three contributions to the Cambro-Ordovician faunas—I The Dikelokephalininae (nov.), its distribution, migration and evolution: Japanese Jour. Geol. Geog., vol. XIII, no. 1–2, p. 163–178.

LERMONTOVA, E. B., 1940, Atlas of the leading forms of the fossil faunas of the U.S.S.R., vol. I—Cambrian: A. Vologdin, editor: State Editorial Office of Geologic Literature, Moscow.

LOCHMAN, CHRISTINA, 1953, Analysis and discussion of nine Cambrian trilobite families: Jour. Paleont., vol. 27, p. 889–896.

NELSON, C. A., 1951, Cambrian trilobites from the St. Croix Valley: Jour. Paleont., vol. 25, p. 765–784.

PALMER, A. R., 1954, The faunas of the Riley formation of central Texas: Jour. Paleont., vol. 28, p. 709–786.

PECK, J. H., & MCFARLAND, H. B., 1954, Whitfield collection types at the University of California: Jour. Paleont., vol. 28, p. 297–309.

POLETAYEVA, O. K., 1936, The fauna of the Cambrian trilobites of the Sanashticgolsk limestone of the West Sayan: Record Geologic of West Siberian Region, no. 35.

RAASCH, G. O., 1952, Revision of Croixian Dikelocephalidae: Illinois State Geol. Survey, Circular no. 179, p. 137–151.

RASETTI, F., 1951, Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains: Smithsonian Misc. Coll., vol. 116, no. 5, p. 1–277.

——, 1952, Ventral Cephalic Sutures in Cam-

brian Trilobites: Am. Jour. Sci., vol. 250, p. 885–898.

SUN, Y. C., 1935, The Upper Cambrian trilobite-faunas of North China: Nat., Geol. Survey of China, Paleont. Sinica, ser. B, vol. 7, fasc. 2, p. 1–93.

——, & SZETU, S. S., 1947, Preliminary notes on the stratigraphy and structure of the Paoshan region, W. Yunnan: Nat. Univ. Peking, Contr. Geol. Inst., no. 32, p. 1–26.

ULRICH, E. O., & RESSER, C. E., 1930, The Cambrian of the upper Mississippi Valley, Part I Trilobita, Dikelocephalinae and Osceolinae: Milwaukee Public Mus., Bull. vol. 12, no. 1, p. 1–122.

——, 1933, The Cambrian of the upper Mississippian Valley, Part II Trilobita, Saukinae: Milwaukee Publ. Mus. Bull., vol. 12, no. 2, p. 123–306.

WALCOTT, C. D., 1914, *Dikelocephalus* and other genera of the Dikelocephalinae: Smithsonian Misc. Coll., vol. 57, no. 13, p. 346–412.

WESTERGÅRD, A. H., 1922, Sveriges Olenidskifer: Sveriges geol. undersökning, ser. Ca, no. 18, p. 1–205.

——, 1953, Non-agnostidean trilobites of the Middle Cambrian of Sweden III: Sveriges geol. undersökning, ser. C, no. 526, Arsb. 46, no. 2, p. 1–60.

WHITFIELD, R. P., 1882, Part III Paleontology: Geology of Wisconsin, vol. IV, 1873–1879, p. 163–204, 341–345.

WHITEHOUSE, F. W., 1939, The Cambrian faunas of northeastern Australia, part 3, the polymerid trilobites: Queensland Museum Mem., vol. 11, pt. 3, p. 179–282.

WILSON, J. L., 1951, Franconian trilobites of the central Appalachians: Jour. Paleont., vol. 25, p. 617–654.

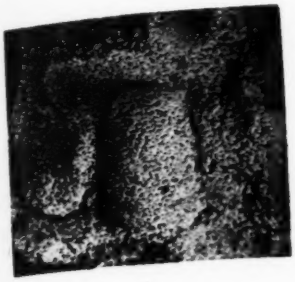
——, 1954, Late Cambrian and Early Ordovician trilobites from the Marathon Uplift, Texas: Jour. Paleont., vol. 28, p. 249–285.

MANUSCRIPT RECEIVED SEPTEMBER 6, 1955.

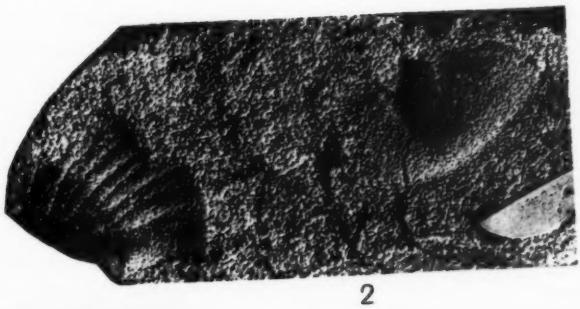
EXPLANATION OF PLATE 47

FIG. *1–4—Briscoia pertransversa* n. sp. *1*, Paratype, incomplete associated cranidium, PUM 43536. *2*, Paratype, impression of nearly complete pygidium and a larger fragment, PUM 78448. *3*, Paratype, a pygidium, PUM 78447. *4*, Holotype, pygidium, PUM 78446. All ×2.2, Franconia formation, *Prosaukia* zone, 1¾ miles SSE of main railroad crossing, North Freedom, Sauk Co., Wis. (p. 460)

5–14—Elkia nasuta Walcott. *6*, *7*, Hypotype, replica and impression of pygidium, USNM loc. 876. *12*, *14*, Hypotype, impression and replica of larger pygidium, USNM loc. 797. *9*, Hypotype, cranidium, USNM loc. 883. *5*,*7*,*10*,*11*,*13*, Hypotypes from *Elkia* coquina in upper zone at Windfall Canyon; *5*, broken free cheek with genal spine, *7*, a medium-sized cranidium, *10*, a hypostome and a large pygidium, *11*, a medium-sized complete pygidium, *13*, a cranidium and fragmentary free cheek. All ×1.1, Eureka district, Nevada. (p. 449)



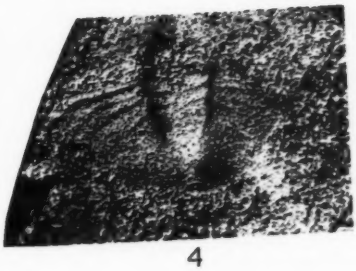
1



2

3

5

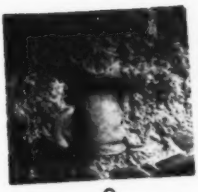


4

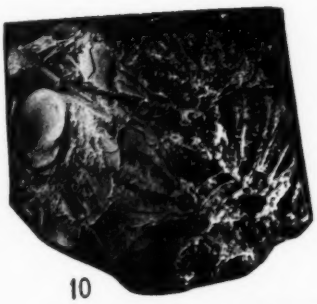
6

7

8

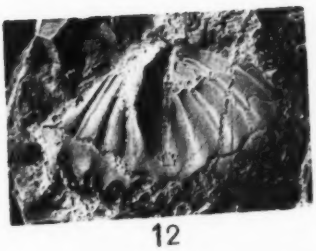


9

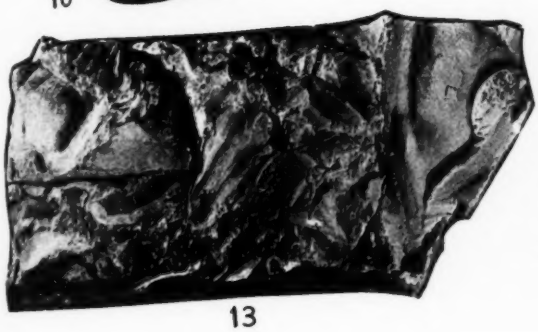


10

11

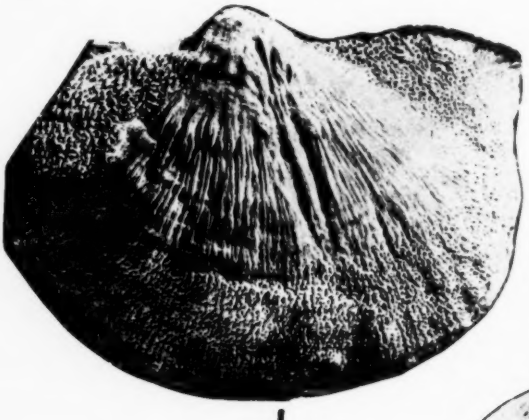


12



13

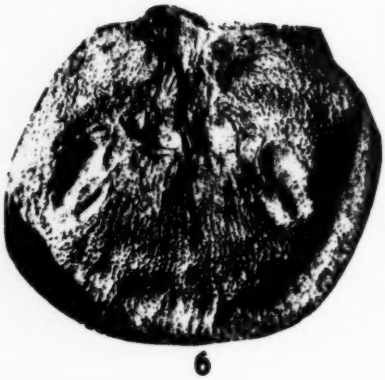
14



1

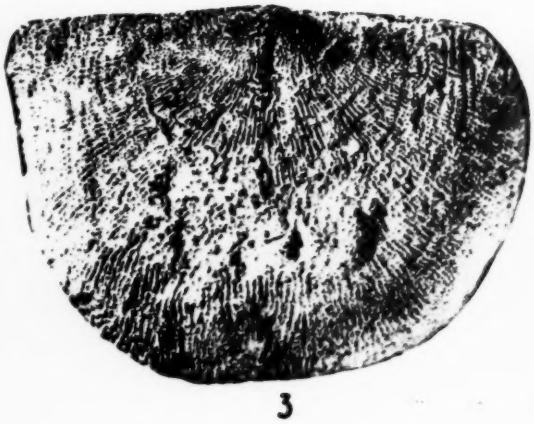
4

5

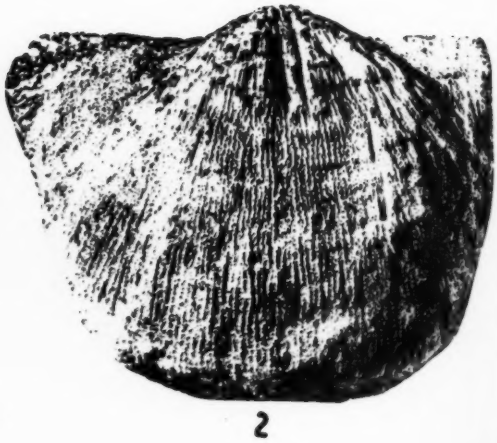


6

7



3



2

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 463–480, PL. 48–50, 5 TEXT-FIG., MAY 1956

SOME CARBONIFEROUS PRODUCTID BRACHIOPODS FROM NEW SOUTH WALES

K. S. W. CAMPBELL
University of New England, Armidale, New South Wales

ABSTRACT.—Species of five genera of productids from the Lower Carboniferous rocks of New South Wales are described. Of these, five are new: *Waagenoconcha delicatula, Pustula abbotti, Pustula gracilis, Echinoconchus gradatus,* and *Linoproductus* sp. In addition, the subspecies *Marginirugus barringtonensis alatus* is described as new. An attempt is made to provide a basis for the use of these genera in elucidating the Lower Carboniferous stratigraphy of New South Wales.

INTRODUCTION

A WIDE variety of genera of productids is distributed throughout the lower Carboniferous marine deposits of New South Wales. No attempt is made herein to give any comprehensive treatment of the group. The five genera studied are of particular interest either from a stratigraphic or zoogeographic point of view, and for that reason have been dealt with in this first paper. *Marginirugus*, for example, has up to the present been recorded only from North America, but now has been identified from beds (mapped in the Upper Burindi Group in N.S.W.) of an age similar to those in which it occurs in America. *Waagenoconcha* is of particular interest because this is its first record from Eastern Australia and because of its occurrence at so low (Tournaisian) a horizon. This also is the first record of *Echinoconchus* in Australia. The two species of *Pustula* described are readily dintinguishable, and since the one (*P. abbotti*) has been found up to the present in rocks of the Lower Burindi Group and the other (*P. gracilis*) in the overlying Lower Kuttung Group, it is likely that further work will show them to be of value in correlation.

The correlation of the stratigraphic groups of the Lower Carboniferous of New South Wales is still in an unsatisfactory state, little critical work having been done on the faunal sequences. Carey and Browne (1938) have suggested the following relationships:

Marine	Terrestrial	Age
	Upper Kuttung Group	Moscovian and higher
Upper Burindi Group	Lower Kuttung Group	Viséan
Lower Burindi Group		Tournaisian

Viosey (1945) has made the most recent attempt to summarise all the information available and has presented his views on the form of correlated columnar sections. This

EXPLANATION OF PLATE 48

All specimens natural size

FIG. *1–3*—*Marginirugus barringtonensis alatus* n. supsp. *1*, internal mould of a pedicle valve; specimen figured pl. XXV, fig. 1 in Dun (1902). *2*, paratype, internal mould of pedicle valve; F. 1564; from same locality as holotype. *3*, holotype, external mould of a brachial valve from Johnson's Hill, Myall Lakes, L.58; F.1547. (p. 467)

4–7—*Marginirugus barringtonensis* (Dun). *4*, mould of a pedicle interior from MacInnes farm section, Barrington, L.42; F.1579. *5*, lateral view of a mould of a pedicle interior; specimen figured pl. XXV, fig. 2 in Dun (1902). *6,7*, mould and cast of brachial interiors from the gap section, Barrington, L.69 and L.70; F.1519 and F.1538. Note the rounded bosses at the anterior edge of the adductor scars in fig. 6 and the large irregular thickenings of the marginal ridge in fig. 7. The cardinal process is broken in both specimens. (p. 465)

(Specimen numbers refer to the University of New England Collections.)

work embodies the results of Carey's and Browne's investigations.

PREVIOUS WORK

The first work on representatives of any of these genera was that of de Koninck, who in 1877 recorded the presence of many European and American productid species in New South Wales. The specimens described as *Productus cora* d'Orbigny are undoubtedly true *Linoproductus*. The description and illustration of the brachial internal of the form which he describes as *Productus punctatus* Sowerby indicate only that it is one of the *Echinoconchus-Psutula-Waagenoconcha* group, no statement of the type of external ornament being given. The localities given are not sufficiently precise to be of any value in obtaining more material. The two forms described as *Productus fimbriatus* Sowerby and *Productus aculeatus* Martin are problematical, and insufficient information is given to be sure of their generic position. The figure of *P. aculeatus*, coupled with the statement in the text that "These tubercles [i.e., the spine bases] often transform themselves into true, longitudinal, irregular rugose ribs," suggests the flattening of the spines to form what appear to be irregular costae in the specimens of *Echinoconchus* described hereunder.

Etheridge Jr. in 1878 recorded the occurrence of *Productus pustulosus* Phillips from the Burindi beds. Since then this specific name has been used to cover a wide variety of forms. Dun (1902) and Osborne (1922, p. 165, faunal list) ascribe to it the species described below as *Waagenoconcha delicatula*, n. sp., while the *Productus pustulosus* Phillips from Zone X (in Voisey 1940, p. 208) has been redescribed by Maxwell (1951) as *Levipustula levis* Maxwell, and that from Zone U is herein placed in the species *Pustula abbotti*, n. sp.

Dun also (1902) described *Productus barringtonensis* Dun, referred below to *Marginirugus*, from the Burindi beds.

No further descriptions were published until 1920 when Benson & Dun described *Productus hemisphaericus* (Sowerby), a *Linoproductus*, from the Babbinboon area, and since then the only records have been in faunal lists.

ACKNOWLEDGMENTS

I wish to acknowledge my indebtedness to Professor A. H. Voisey, for assistance in the field, and to Dr. Dorothy Hill for advice on the preparation of this work.

SYSTEMATIC PALEONTOLOGY

Genus MARGINIRUGUS Sutton

Marginirugus SUTTON, 1938, Jour. Paleont., vol. 12, p. 559–651, pl. 63, fig. 10–13.
Marginirugus Sutton. SUTTON & SUMMERSON, 1943, Jour. Paleont., vol. 17, p. 325–326, pl. 54, fig. 1.

Genotype.—*Productus magnus* Meek & Worthen.

Diagnosis.—Shell large; globose; costate; concentric ribs on the auriculations and posterior of the valves; visceral cavity deep; visceral portion of brachial valve flat; margin of visceral disc thickened, the thickening in most cases not rising above the plane of the visceral disc, though a slightly elevated ridge may occasionally occur; cardinal process projecting ventrally and extending only a short distance beyond the hinge.

Remarks.—Sutton (1938) has given an excellent description of the genus based upon the one species *P. magnus* Meek & Worthen. There are a few points of difference between the genotype and *M. barringtonensis* (Dun), but these are not considered to be of generic importance, and hence the interpretation of the genus given by Sutton is broadened to include species of the latter type.

Firstly, Sutton states that the ridge "does not rise above the general level of the brachial disc," and his figure 1g conveys the impression of symmetrical curvature over the edge of the visceral disc. Among the specimens of *M. barringtonensis* (Dun) from one locality there are specimens of this type but variation is broad and there are other forms, which exhibit well developed ridges rising above the general surface of the valve. This does not make the ridge marginiferid in type however as the main thickening takes place in the manner described by Sutton.

Secondly, although the cardinal process extends sharply ventrally and does not project far beyond the hinge-line as is the condition in *M. magnus* (Meek & Worthen),

it never exhibits the irregularities of growth exhibited by that species. The posterodorsal surface is regularly trifid while the ventral surface is usually slightly bilobed at its extremity.

Thirdly, and least important, the brachial scars of *M. magnus* are in the anterior part of the valve, but in *M. barringtonensis* their position is variable about the midline.

This genus bears a superficial similarity to some groups which are included within the genus *Gignatoproductus* Prentice, and described by Sarytcheva and Paeckelmann under the name *Gignatella*, e.g., the group of *Gigantella striato-sulcatus* (Schwet.). Wherever the brachial valves of these forms are illustrated they follow the contours of the pedicle valves much more closely than do those of *Marginirugus* and there is no indication of thickening around the margins of the brachial visceral disc. Moreover the arrangement of the spine bases on the cardinal margins of the two forms is not comparable and the relationship between these two genera remains obscure. No *Marginirugus* has yet been described from Europe or Asia, and the only *Gignatoproductus* in North America are "restricted to the far west and Alaska and mark a fauna of strong Asian affinities" (Weller, et al., 1948, p. 115). *Gigantroproductus* also appears to be a later development than *Marginirugus*.

Range.—So far as is known the genus in North America is restricted to an horizon which is assigned variously to the Keokuk and Warsaw limestones. Laudon (1948) has made out a good case for the inclusion of the Warsaw limestone in the Osagean, and for the correlation of the Osage-Meramec boundary with the Tournaisian-Viséan boundary of Europe. If this work is reliable then regardless of whether *M. magnus* occurs in the Keokuk or Warsaw, its horizon is probably to be correlated with one at the top of the Tournaisian. *M. barringtonensis* (Dun) is found in the lower part of the Upper Burindi Group which has in the past been regarded as Viséan in age. The associated fauna is very poor, being restricted to species of chonetids and unidentifiable spiriferids. In Australia, as in America, the genus is always restricted to a narrow zone, but correlation between the two continents would be impossible without confirmatory evidence from associated faunas. This evidence will not be forthcoming until localities with richer faunas are discovered in New South Wales.

MARGINIRUGUS BARRINGTONENSIS (Dun)
Pl. 48, fig. 4–7; Pl. 49, fig. 7–9; Pl. 50, fig. 10–11; Text-fig. 1,2

Productus barringtonensis DUN, 1902 (in part), Rec. Geol. Surv. N. S. Wales, vol. 7, pt. 2, p. 91–93, pl. XXV, fig. 2–5, non fig. 1.
Productus barringtonensis Dun. VOISEY, 1940, Proc. Linn. Soc. N. S. Wales, vol. 65, p. 197.

Lectotype.—(here selected) F. 37308 Australian Museum Collection. Specimen figured by Dun 1902, Pl. XXV, fig. 3.

Description.—External structure: The shell is large. The pedicle valve is inflated (see Text-fig. 1) and is most strongly convex posteriorly. The umbo is pointed and slightly overhangs the hinge which is long and straight, being the maximum width of the valve. The cardinal extremities are usually more or less rectangular, but they may be slightly extended. The valve is globose in posterior aspect, the lateral slopes being almost vertical. The ears are not sharply differentiated from the body of the valve. The ornament consists of rather regular costae, and of spines which are small and sparse on the visceral portion of the valve but much more powerful and frequent along the cardinal margin and around the trail. The cardinal spines increase in size away from the umbo, while those on the trail are very long and thick. Concentric wrinkling is prominent on the ears but decreases over the visceral disc.

The brachial valve is variable in longitudinal section from evenly rounded to almost geniculate, while in outline it is subsemicircular. The umbo is distinctly concave and the ears poorly differentiated. Ornament consists of well developed costae and concentric wrinkles. The wrinkling is poorly developed around the umbo and becomes stronger anteriorly and laterally, on the visceral disc, but is weak on the lateral parts and absent on the anterior parts of the trial. The costae are usually slightly wavy, and may become irregular on the trail. There are 12 to 17 costae per 10 mm. on the trail, the average being 14. The valve is aspinose.

Internal structures: The pedicle valve is thickened along the hinge, and occasionally this thickening is extended on to the lateral portions of the visceral disc. The umbo is also slightly thickened. The adductor platforms are narrow, slightly elevated and are wholly or partly divided by a low median ridge which arises in the umbonal callosity.

TEXT-FIG. *1*—Sections through pedicle valves of *M. barringtonensis* to illustrate the curvature of the valves.

The divaricator scars are never well defined, but are large, flagellate and longitudinally striated. Much of the interior of the valve is costate, the costae in adult specimens bearing very fine pustules. In some specimens in which this costation is reduced the pustules have an irregular arrangement.

The brachial valves are strongly thickened. Most specimens have a slight cardinal ridge parallel with the hinge line. The lateral and anterior margins of the visceral disc are excessively thickened, in some cases a marked ridge rising above the general level of the interior surface. This marginal ridge may bear coarse irregular rugosities. The squat cardinal process extends only slightly posterior to the hinge line. Its posterodorsal surface is markedly trifid and is set at a high angle to the plane of the valve, and the ventral surface is evenly rounded or slightly bilobed at its extremity. The median septum is very broad at the base of the cardinal process, and it may taper off gradually toward the anterior, or it may decrease in width suddenly at the posterior edge of the adductor scars. Beyond this point the septum is usually simple, but in a few specimens it bears a distinct, sharp median groove on the portion between the adductor scars. The length of the median septum is approximately three-quarters the length of the visceral disc. Its height is very variable. The adductor scars are large and dendritic, and are borne on platforms that are very variable in height. Some specimens exhibit large unmarked callosities on the anterior portion of the adductor platforms. The brachial impressions, too, are very distinct but are variable in form.

Remarks.—Dun's original specimens are from the "Washtubs" near Barrington. The above description is based on topotype material collected by the author, and on a set of excellent photographs provided by Dr. Walkom of the Australian Museum, Sydney. It is unfortunate that at the type locality, whilst there is an abundance of brachial valves, pedicle valves are remarkably rare. Because of this the description of that valve has been rather sketchy.

The variation exhibited in the development of the marginal ridges in the brachial valve is probably a reflection of age variation. There is an enormous range of variation in this character at each locality, but all

TEXT-FIG. *2*—Longitudinal sections of specimens of *M. barringtonensis* to illustrate the development of the marginal thickening of the brachial valve.

the forms which show thickened marginal ridges also exhibit thickening of other structures such as the branchial scars and the anterior portion of the adductor platforms. This may be a gerontic development.

The resemblance of *M. barringtonensis* to *M. magnus* is most striking and there is no doubt that they are closely related. With regard to the differences in the form of the

cardinal processes of the two species mentioned in the generic remarks, it is worthy of note that a photograph of *M. magnus* supplied to me by Dr. G. A. Cooper, shows a cardinal process indistinguishable from the normal type of *M. barringtonensis*. A further point of distinction may be in the spread of the brachial scars. In the only specimen of *M. magnus* available to me the ratio of the distance between the outer margins of the brachial scars to the width of the visceral disc is approximately 0.66 whereas the mean for 14 specimens of *M. barringtonensis* is 0.79 and the range of variation 0.72–0.93.

MARGINIRUGUS BARRINGTONENSIS ALATUS, n. subsp.

Pl. 48, fig. 1–3; Pl. 49, fig. 10; Text-fig. 3

Productus barringtonensis DUN, 1902 (in part), Rec. Geol. Surv. N. S. Wales, vol. 7, pt. 2, p. 91–93, pl. XXV, fig. 1, non fig. 2–5.

Productus barringtonensis Dun. OSBORNE, 1950, Mem. Roy. Soc. N. S. Wales, Mem. 1, p. 29.

Holotype.—F. 1547, University of New England Collections.

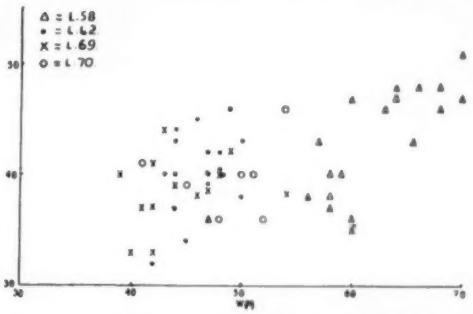
Locality.—Johnson's Hill, Myall Lakes.

Description.—This subspecies may be readily distinguished from typical *M. barringtonensis* by its much more extended hinge line, its smaller cardinal process, the much less robust posterior portion of its brachial median septum, and the larger size of the adults.

Remarks.—The dimensions of the hinge line of this subspecies have been compared with those of typical *M. barringtonensis* and the differences found to be statistically significant (See under dimensions). This, together with the differences cited above warrant the erection of a new subspecies.

The type locality of this new subspecies is distant some 8 miles from the nearest known outcrop yielding *M. barringtonensis* at Booloombayt, though this distance may be appreciably reduced by further field work. The stratigraphy of the area is not sufficiently well known to state whether there is any significant time interval between the beds at the two localities, but the work which has been done (Osborne, 1950, and Voisey, 1940) suggests that they are approximately on the one horizon.

There is evidence to suggest that the two forms may be ecologically as well as geographically isolated. Firstly, the subspecies *M. b. alatus* is associated with a rich chonetid fauna, in which, although the valves are always separated, preservation is usually excellent. Also the sediments at this locality are slightly finer than at either locality at which typical *M. barringtonensis* is found, and these two factors taken together suggest a somewhat quieter environment in the Myall Lakes region. It is possible that the relatively small cardinal process and supporting median septum found in subspecies *M. b. alatus* can be correlated with this quieter environment. The functional significance of the longer hinge line is unknown. It seems possible that here we have an example of true ecological subspeciation. This hypothesis is lent some support by the fact that in Dun's syntypes of *M. barringtonensis* there is one specimen (Pl. XXV, Fig. 1, now F. 35466 Australian Museum Collection) with a broad, alate hinge line. This specimen is labelled "near Barrington". The only two other specimens I have examined from this locality are similar. They are preserved in a fine black sandstone, which must have been deposited in a very quiet environment.



TEXT-FIG. 3—Scatter plot of length/width of hinge of *M. barringtonensis* and its subspecies *M. b. alatus*.

It is interesting to note that some of the specimens of *M. magnus* are alate in quite the same manner as this subspecies.

Dimensions.—(All measurements in millimeters.)

Internals of the brachial valve of *M. barringtonensis barringtonensis*

Locality	Length of visceral disc	Length of adductor scars	Length of median septum	Width of visceral discs	Width of adductor scars	Width of* brachial scars
L. 42	41	15	31	48	17	—
	44	15	34	56	20	42
	37	11	29	—	21	37
	32	12	24	46	14	38
L. 49	46	16	36	55	18	42
	39	13	32	50	16	38
	38	10	28	44	15	34
L. 69	38	10½	31	56	20	42
	32	10	24	44	13	34
	37	12	26	46	20	36
	41	12½	32	45	18	35
	39	12½	—	50	17	37
	37	14	25	45	18	42
	33	11½	27	42	15	36
	33	11½	23	42	15	35
L. 70	43	14	33	60	21	46
	Internals of brachial valve of *M. barringtonensis alatus*					
L. 58	—	13	—	45	10	—
	50±3	21	34	66	19	—

* Distance between the extreme outer limits of the brachial scars.

Internals of the pedicle valve of *M. barringtonensis barringtonensis*

Length of curvature	Width at hinge	Greatest width	Length of adductor scars	Width of adductor scars
82±	47±	52±	—	–
90±	44±	—	36	4
105±	48	59±	49	–
83	37	46	30	–

Explanation of Plate 49

All specimens natural size unless otherwise stated

Fig. *1–3*—*Pustula gracilis* n. sp. *1*, holotype, mould of pedicle interior from 200 yards upstream from Cameron's Bridge, Rouchel Brook, L.57; F.1447. *2a,b*, paratype, plaster cast of pedicle exterior and mould of brachial exterior; F.1446A and B. *3a,b*, paratype, plaster cast of brachial interior and mould of brachial exterior; F.1450B and A. (p. 477)

4–6—*Pustula abbotti* n. sp. *4*, paratype, mould of pedicle interior; F.1433. *5a,b*, holotype, moulds of pedicle and brachial interiors; from Nooroo, L.55; F.1431A and B. *6*, paratype, mould of brachial exterior; F.1432. (p. 476)

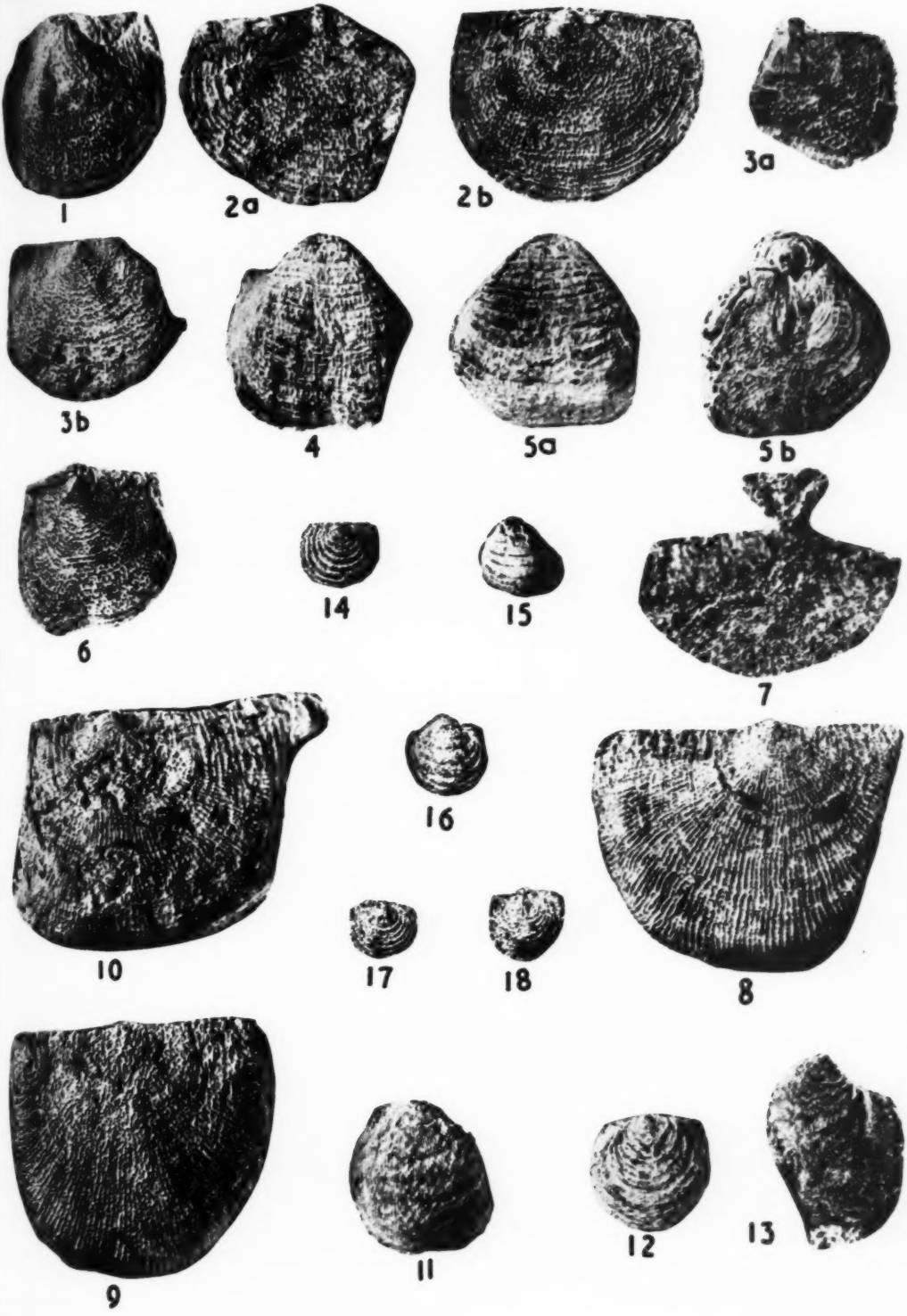
7–9—*Marginirigus barringtonensis* (Dun). *7*, plaster cast of the posterior surface of a cardinal process from Booloombayt, L.49; F.1516, ×2. *8,9*, moulds of brachial exteriors from gap section, Barrington, L.69; F.1542 and F.1578. (p. 465)

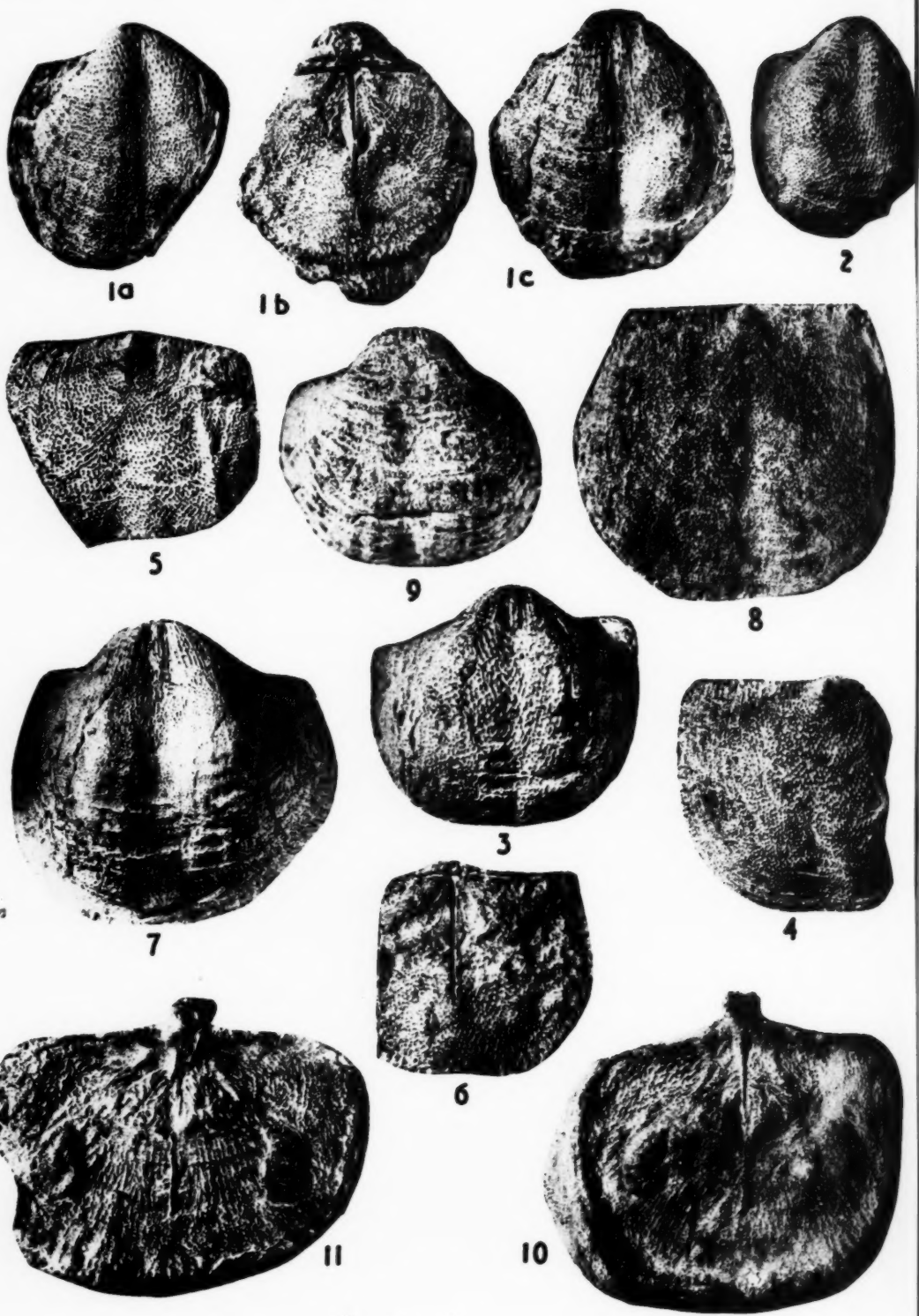
10—*Marginirigus barringtonensis alatus* n. subsp. Mould of brachial exterior showing alata structure; from Johnson's Hill, Myall Lakes, L.58; F.1546. (p. 467)

11–13—*Linoproductus* sp. *11*, mould of pedicle interior from Nooroo, L.55; F.1630. *12,13*, mould of brachial exterior and plaster cast of pedicle exterior; from Babbinboon, L.35, F.1617 and F.1618. (p. 479)

14–18—*Echinoconchus gradatus* n. sp. *14*, paratype, mould of brachial exterior; F.1631. *15*, holotype, partly decorticated pedicle valve from Babbinboon, L.35; F.1609. *16*, paratype, pedicle interior; F.1611. *17,18*, paratypes, plaster casts of brachial interiors; F.1603 and F.1584. (p. 474)

(All paratypes are from the same localities as the holotypes.)


1
2a
2b
3a
3b
4
5a
5b
6
14
15
7
10
16
8
17
18
9
11
12
13


1a
1b
1c
2
5
9
8
7
3
4
6
11
10

Comparison of length/width ratios of the brachial valves of *M. barringtonensis barringtonensis* and *M. b. alatus*.

	Mean of L/W	S.D.	No. of specimens	Range
M. b. barringtonensis	0.87	0.083	36	0.75–1.05
M. b. alatus	0.69	0.052	19	0.59–0.77

In the above length/width ratios only those forms considered to be adult have been analysed. There appears to be no secure basis for the estimation of adulthood, such as counting of successive growth rings, in these specimens, and so a convenient arbitrary length minimum (viz. 32 mm.) has been chosen.

In order to test the significance of the difference between the means, Student's "t" has been calculated using the small sample method of Simpson & Roe (1939, p. 205). In this case $t = 9$ approximately, which is highly significant.

Localities.—(All L. numbers refer to the University of New England Collection.)

L. 42 MacInnes farm section, Gloucester trough, near Barrington; good reference 947-420, Gloucester One Mile Military Sheet.

L. 49 Booloombayt section; grid reference 293-976, Bullah Delah One Mile Military Sheet.

L. 58 Johnson's Hill, Myall Lakes; grid reference 370-836, Bullah Delah One Mile Military Sheet.

L. 69 Gap section near Barrington; grid reference 933-383, Gloucester One Mile Military Sheet.

L. 70 Grid reference 940-380, Gloucester One Mile Military Sheet.

Genus WAAGENOCONCHA Chao

Waagenoconcha CHAO, 1927, Paleont. Sinica, (B) vol. 5, no. 2, p. 85–93, pl. 7, fig. 3–8; pl. 15, fig. 2–4.

Genotype.—*Productus humboldti* d'Orbigny.

Diagnosis.—Small to medium-sized productids; thin-shelled; pedicle valve rather evenly convex, sinuate; brachial valve flat or concave and with a median fold arising anterior to a concave umbo; surface bearing numerous, small, quincuncially arranged spines, which become finer on the adult stages of both valves; the interior margin of the brachial visceral disc may or may not bear thickening of the shell.

Range.—The genotype is from the Upper Carboniferous of Bolivia. In North America the genus is usually regarded as being restricted to the Permian (Cooper, 1944) though it is possible that *Krotovia praecursor* Stainbrook may be a *Waagenoconcha*.

In Russia, Ivanov (1935) records that "within the region of Moscow the representatives of the genus *Waagenoconcha* occur in the Upper Carboniferous." (English summary). Tschernyschew figures *Productus humboldti* d'Orbigny and *Productus irginae* Stuckenberg from the Upper Carboniferous of the Urals. Nalivkin, 1937 (English summary) records forms which he refers to *Waagenoconcha* in beds ranging from Fammenian to Viséan. Unfortunately, the figures of the species in question were too poor in the only (photostat) copy of the paper available for me to give an opinion of their affinities.

EXPLANATION OF PLATE 50

All specimens natural size unless otherwise stated

FIG. *1–9*—*Waagenoconcha delicatula* n. sp. *1a–c*, holotype, plaster cast of the pedicle exterior; moulds of the brachial and pedicle interiors from Hilldale, L.53; F.1405. *2*, paratype, plaster cast of pedicle exterior; F.2361. *3*, paratype, mould of pedicle interior; F.1379. 4 and 5, paratypes, moulds of brachial exteriors; F.1391 and F.2362. *6,7*, paratypes, moulds of brachial and pedicle interiors; F.1399 and F.2363. *8,9*, mould of a brachial exterior and a partly decorticated pedicle valve from Babbinboon, L.35; F.1414 and F.1415. Paratypes from same locality as holotype. (p. 471)

10–11—*Marginirugus barringtonensis* (Dun). Plaster casts of brachial interiors from Booloombayt, L.49 and the gap section, Barrington L.69; F.1500 (×15/16) and F.1515. (p. 465)

In China, Chao records the genus as "chiefly developed in the Upper Carboniferous and Permian," whilst in India it has been recorded from the *Productus* limestones and the Anthracolitic slates.

In Australia the genus has been previously described only from the Permian of Western Australia by Prendergast (1943). The present record is the first from eastern Australia.

Remarks.—The genera *Krotovia* and *Waagenoconcha* belong to closely related stocks, which are distinguished chiefly by the arrangment of the spines and the presence or absence of a sinus in the pedicle valve. There are some forms which exhibit a semi-quincuncial arrangment of spine bases and a flattened or incipiently sinuous pedicle valve. Stainbrook (1947) dealt with this problem in his remarks on *Krotovia praecursor* from the Percha shale and stated

> The nearly quincuncial arrangement of the spines and the medial flattening or sulcus of the pedicle valve might indicate that this species should be assigned to *Waagenoconcha*, but that genus is reported only from the Permian.

K. praecursor, moreover, bears finer spine bases towards the margins than on the posterior part of the shell, a characteristic of *Waagenoconcha*.

A quincuncial or semi-quincuncial arrangement of spine bases has been observed on other productids from the lower Carboniferous of various areas, some of these forms possessing a flattened or sinuate venter on the pedicle valve as in *Waagenoconcha*, and others possessing a rounded venter as in *Krotovia*. For example, Thomas (1914, p. 279) records that *Pustula subpustulosa* from the Tournaisian of England has obscure banding of the pedicle valve and the spine bases are "more or less quincuncially arranged." A semi-quincuncial arrangement of spine bases is associated with a sinuate shell in *P. pilosa* described and figured by the same author (especially Pl. XX fig. 4), though in this species concentric banding is still obvious; and Paeckelmann described from the German Lower Carboniferous *Productus* (*Krotovia*) *spinulosus* Sowerby, which has spines arranged more or less strongly in quincunx.

Pustula fredericksianus Paeckelmann, from the Tournaisian and lower Viséan of Germany, has a semi-quincuncial arrangement of spine bases which also become finer towards the anterior and lateral margins. Paeckelmann (1931, p. 145) discussed the relationships between *P. fredericksianus*, *P. pilosa* and *Waagenoconcha humboldti* and considered that at the most, the latter could be considered as a specialized decendent of *P. pilosa*.

The generic status of *W. delicatula*, n.sp., is complicated firstly by the existence of a marginal thickening around the visceral disc of the brachial valve, such thickenings having been taken of recent years to be of considerable taxonomic value, and secondly by the fact that it occurs in such a low stratigraphical position. So far as I have been able to ascertain no such thickening has been described in undoubted specimens of *Productus humboldti* d'Orbigny, although this may possibly be due to omission in description, as specimens of *P. humboldti* figured by Kozlowski bear coarser spines around the interior margin of the brachial valve, and these usually occur where there is a thickening of the shell, for example, as in *Productus irginae*. Moreover, specimens of *Productus irginae* Stuckenberg, from the Upper Carboniferous of Russia (Tschernyshew, 1902, Pl. LII, fig. 1c, 1d) show slight thickening associated with coarser spines around the anterior edge of the brachial disc. This species is customarily referred to the genus *Waagenoconcha*, and it is of an age comparable with that of *W. humboldti*.

It is of considerable importance also that Ivanov (1935 English summary) in a generic description of *Waagenoconcha* records that

> Two flat ridges diverge from the base of the process forming acute angles with the hinge-line, and passing on the sides of the valve into a feeble ridge which skirts the valve.

His specimens also were of Upper Carboniferous age. Some doubt, however, is cast on the generic determination of his specimens since he states a fissure like area to be present in the ventral valve, and no area is present on the genotype or any related species. It is possible, however, that Ivanov mistook for an area the grooved articulating surface that exists on some pedicle valves.

Nevertheless, the present author is of the opinion that marginal thickening of the visceral disc of the brachial valve is not always of generic taxonomic value, since it may or may not occur in obviously closely knit stocks; e.g., certain species of *Pustula*, such as *Pustula pyxidiformis* (de Koninck) and *Pustula pustulosa* (Phillips) as described by Thomas (1914), are with and without marginal thickening respectively; and *Strophalosia kimberleyensis* Prendergast (Prendergast, 1943) bears a marginal thickening not recorded in most other members of the genus.

Hence I am of the opinion that to create a new generic name for this species or to refer it to either *Pustula* or *Krotovia* would be to withdraw attention from its essential relationships, and that the correct procedure is to recognize that productids of waagenoconchid, pustulid and krotoviid affinities were developing contemporaneously in the Lower Carboniferous.

From the above observations it would appear that at least some waagenoconchids have developed from krotoviid types by the development of a median sinus and from pustulid types by the reduction of the concentric ribs, in both groups evolution, also occurring towards a quincuncial arrangement of spine bases. There is also the possibility that waagenoconchid forms were developed independently, since they have been found very early in productid history before the other stocks became firmly established.

It may be pertinent to note here that other groups of concavo-convex brachiopods also develop marginal thickenings in the brachial valves without such developments being regarded as of more than specific value, e.g., the genus *Rafinesquina* includes *R. ponderosa* Hall with a heavy marginal callosity, and *R. trentonensis* Conrad without any such feature.

Waagenoconcha delicatula, n. sp.
Pl. 50, fig. 1–9; Text-fig. 4,5

Productus pustulosus Phillips. Dun, 1902, Rec. Geol. Surv. N. S. Wales, vol. 12, pt. 2, p. 75–77, pl. 23, fig. 1–3,14.

Productus pustulosus Phillips, Benson & Dun, 1920, Proc. Linnean Soc. N. S. Wales, vol. 45, pt. 3, no. 179, p. 344.

Productus pustulosus Phillips, Osborne, 1922, Proc. Linnean Soc. N. S. Wales, vol. 47, pt. 2, p. 165.

Holotype.—F. 1405 University of New England Collections.

Description.—External structure: The pedicle valve has its greatest width at the mid length of the valve. The hinge line is only slightly shorter than the greatest width. The umbo is acute and strongly overhangs the hinge line which is slightly thickened and bears a faint articulatory groove. The ears are not sharply differentiated from the body of the valve, but gradually merge into it. The lateral slopes are very steep. The median sinus is broad and distinct on the posterior, but becomes progressively narrower, shallower and less well defined on the anterior half of the valve. The surface is marked by numerous small quincuncially arranged spine bases which are coarsest over the juvenile, and finer and more abundant over the adult portions of the valve. Masses of hair-like spines occur on the ears. Concentric markings are obscure except on the ears, and in some specimens, the anterior portions of the valve. The larger spine bases are elongate, but the smaller are almost equidimensional.

The brachial valve is concave, sometimes strongly so. The umbo is distinct and strongly concave. A median fold is well developed. It arises in the posterior fifth of the valve and becomes progressively higher anteriorly. The spine bases are fine on the umbo, coarse on the central part and fine on the anterior and lateral margins. The spine bases are rarely elongated, most of them being very small and equidimensional. Very fine concentric growth lamellae cover the whole valve.

Internal Structure: The pedicle valve has distinct, faintly dendritic adductor scars situated on low, narrow platforms. A faint median septum divides the muscle scars, but does not reach to the umbo. The divaricator scars are longitudinally striate, broad, flabellate and indistinctly defined. The interior of the valve in juveniles exhibits quincuncially arranged depressions corresponding in position with the external spines, but in adults there is a tendency to reduce considerably the size of these pits and destroy their quincuncial arrangement

over the juvenile portion of the shell. Gerontic forms produce a series of coarse irregular pustules around the anterior margins.

The brachial valve has high, narrow cardinal ridges given off from the base of the cardinal process and extending along the hinge to the cardinal extremities. A strong median septum extends approximately two-thirds of the length of the valve. The cardinal process is rather small, bifid on its posteroventral surface, trifid on its whole dorsal surface, and directed approximately in the plane of the valve. The adductor scars are large and dendritic, and are situated on subtriangular platforms which in juveniles and normal adults are slightly elevated anteriorly. Specimens which apparently have reached the gerontic stage may have the anterior portion of the adductor platform raised into a large rounded boss. A slight marginal thickening occurs in most specimens, and in gerontic forms this is increased to a definite ridge. No brachial markings have been observed. The interior of the valve is covered by a series of fine quincuncially arranged pustules which become very coarse around the anterior edges of gerontic forms.

Dimensions.—(All measurements in millimeters.)

Pedicle valves, specimens from L. 53 (type locality)

Length	Width	Length of adductor platforms	Width of adductor platforms
44	43	ca. 11	6
38	40	10	5
48	52	14	7
25 (juv.)	31	—	—
41	44	14	—
	Specimens from L. 51		
44	43	15	7
37	39	—	—
	Specimens from L. 35		
ca. 43	ca. 44	ca. 13	5
ca. 40	ca. 41	—	—
ca. 28 (juv.)	ca. 34	—	2½

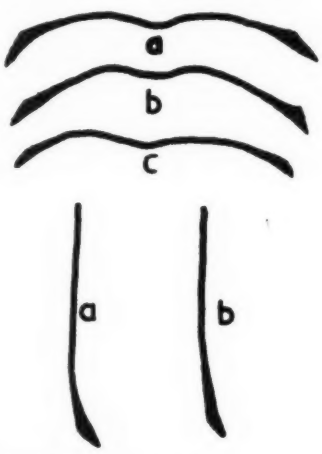
Brachial valves, specimens from L. 53 (type locality)

Length	Width	Length of adductor platform	Width of adductor platform	Length of median septum
36	41	12	10	22
30	42	11	9	19
24	33	8	5	12
33	40	12	10	20
28	36	—	—	—
32	41	—	—	—
32	44	—	—	—
31	41	13	7	18
	Specimens from L. 51			
ca. 34	43	—	—	—
35	45	—	—	—
	Specimens from L. 35			
30	38	ca. 10	—	20
32	—	ca. 10	ca. 6	20
33	—	10	—	17
36	46	—	—	—
29	34	—	—	—
43	51	—	—	—
44	52	—	—	—

Variation.—Specimens from the type locality: The spine bases on the pedicle valve vary in their degree of coarseness on different parts of the valve, for while in some specimens there is a gradual decrease in size from anterior to posterior, in others there appears to be a sudden change in size at about the mid-valve position. The brachial valve varies from faintly to rather strongly concave, the actual degree of concavity being difficult to measure because of distortion and other factors of preservation. This variability may be a function of the stage of growth, the more adult specimens being the more concave, but insufficient material is available to be certain of this.

Markings on the interior of the valves also are very variable. The pedicle valves of some specimens exhibit multitudinous, irregularly arranged, minute depressions over all stages but the adult where coarser irregular pustules occur, whilst other specimens exhibit quincuncially arranged eminences over the whole inner surface. The interiors of the brachial valves, of adults at least, bear exceedingly few depressions on the postero-lateral portions, and pustules which become progressively coarser towards the margins, on the remainder of the valve.

Specimens other than those from the type locality: The specimens from near Clarencetown (marked L. 51 and L. 64) are undoubtedly conspecific with *W. delicatula*.



TEXT-FIG. 4—Sections through the brachial valve of *Waagenoconcha delicatula* showing the nature of the marginal thickening; transverse and longitudinal sections.

TEXT-FIG. 5—Transverse and longitudinal sections through three pedicle valves of *W. delicatula*.

A group of specimens from Babbinboon (marked L. 35), bears a close resemblance to this species, although there are minor differences. The pedicle valves of the Babbinboon material, for example, exhibit concentric banding much more clearly than *W. delicatula*, and this suggests the possibility that they ought to be assigned to either *Pustula* or *Echinoconchus*. The brachial valves show no marked concentric banding. Although the preservation of externals is poor and the distribution of spines cannot be studied in detail, wherever spines have been observed, they are uniformly fine, and not differentiated into distinct size groups. This rules out the possibility of the species being an *Echinoconchus*, but no clear evidence has been obtained to rule out the possibility of its being a *Pustula*.

Part from this banding of the pedicle valve, and a difference in the size of the brachial adductor scars, these specimens are remarkably similar to *W. delicatula*, and to assign them thus appears to be the most satisfactory procedure.

Several distorted specimens from Nooroo, near Stroud, marked L. 54 and L. 55, appear to be related to this species, but they are too poorly preserved for accurate identification.

Localities.—(All L. numbers refer to the University of New England Collection.)

L. 35 Hillside at Babbinboon; grid reference 570-637, Attunga One Mile Military Sheet.

L. 51 and L. 64 Ridge west of the road about 2 miles north of Clarencetown; grid reference 803-735, Paterson One Mile Military Sheet.

L. 53 Hilldale; grid reference 660-790, Paterson One Mile Military Sheet.

L. 54 and L. 55 Railway cutting near Nooroo; grid reference 903-985 Dungog One Mile Military Sheet. These localities are close together in the cutting.

L. 35, L. 51, L. 64 and L. 53 are all known to be in the topmost beds of the Lower Burindi Group. The stratigraphical position of L. 54 and L. 55 is indefinite, but they are thought to be within the upper half of the Lower Burindi Group.

Genus ECHINOCONCHUS Weller

Echinoconchus WELLER, 1914 (in part), State Geol. Surv. Illinois, Monograph 1; p. 138–142, pl. 17, fig. 1–7, 10–15; pl. 18, fig. 1–6.
Echinoconchus Weller. PAECKELMANN, 1931, Abh. Preuss. Geol. Landesanst., (n.f.) vol. 136, p. 152–172, pl. 15, fig. 7–10; pl. 16, fig. 1–13; pl. 17, fig. 1–7.
Echinoconchus Weller. SUTTON, 1938, Jour. Paleont., vol. 12, p. 555–557, pl. 66, fig. 1–6.

Genotype.—*Productus punctatus* Sowerby, 1822. Muir-Wood (1951) has made application to the International Commission of Zoological Nomenclature for this species to be referred to Sowerby, 1822, as a result of the invalidation of Martin's original species *Conchyliolithies Anomities* (*punctatus*) by the Commission in 1948. This redesignation does not affect the discussion of the genus given by Muir-Wood, and it is used here in anticipation of its adoption by the Commission.

Remarks.—The status of this genus has been discussed by Sutton (1938), who has given an adequate summary of its history and present standing, and the present author accepts his conclusions concerning the interpretation of the genus.

The generic status of the *Productus elegans* group is somewhat problematical as has been pointed out by Yanishevsky, Mansuy, and Chao. Paeckelmann (1931) also separates this group from a group typified by the genotype. The group, consisting of *E. elegans* (McCoy), *E. venustus* (Thomas), *E. eximus* (Thomas), *E. exquisitus* (Thomas), *E. crameri* Paeckelmann and *E. gradatus* n. sp. is small and closely compact and is readily distinguished from the genotype by the small size of its members and their lack of a median sinus and fold. Chao (1927, p. 67) mentions differences in external ornament and also states that "In regard to their internal structures [i.e., of *E. punctatus* and *E. elegans*] they are still more diversified," but he does not state what he regards to be the significant differences. In the author's opinion the internal structures of the two species are quite similar, and there appears to be no basis for the generic separation of the *E. elegans* group from the *E. punctatus* group as suggested by Chao, except for the differences in size and the absence of a sinus and fold in *E. elegans*. Since both groups are co-extensive in space and time, there appears to be no necessity at the present time to raise the *E. elegans* group to generic rank. It is worthy of note that Muir-Wood (1948) also continued to refer the group to *Echinoconchus*.

Range.—In Britain, Thomas (1914) has recorded *E. elegans* itself from horizons ranging from C_2 to D_3 and perhaps as high as the Millstone Grit. Other related species, viz. *E. venustus* (Thomas), *E. subelegans* (Thomas), *E. eximus* (Thomas) and *E. exquisitus* (Thomas) are all Viséan in age.

The German members of the group as recorded by Paeckelmann, *E. elegans* (McCoy), *E. crameri* Paeckelmann, *E. venustus* (Thomas), *E. subelegans* (Thomas), and *E. eximus* (Thomas) occur within the Viséan.

In North America *E. biseriatus* (Hall) has been recorded from the Salem limestone by Weller (1914) (lower Viséan, Weller et al., 1948) and from the Moorefield shale (Tournaisian-Viséan) boundary.

Yanishevsky has recorded *E. elegans* from the Viséan of Turkestan, and Chao has recorded the same species from the Viséan of Kansu. In the present author's opinion this latter determination is incorrect. Chao also records the species as occurring rarely in the Taiyuan and Penchi Series of North China, and this occurrence, if confirmed, would be the youngest known.

ECHINOCONCHUS GRADATUS n. sp.
Pl. 49, fig. 14–18

Posidoniella ? spp. indet., BENSON & DUN, 1920, Proc. Linnean Soc. N. S. Wales, vol. 45, pt. 3, no. 179, p. 354, pl. 23, fig. 6.
Productus muricatus (Phillips), BENSON & DUN, 1920 (in part), ibid., pl. 23, fig. 1.

Holotype.—F. 1609 University of New England Collections.

Description.—External structure: The pedicle valve is small and gibbous, and is almost as wide as it is long. The hinge is equal to the greatest width of the shell. The valve is almost semicircular in both lateral and anterior profiles. The umbo is prominent and strongly incurved. Strong concentric ribs are developed, there being between

five and seven ribs per 10 mm. on the median anterior portion of the valve. The small, slightly depressed auriculations bear much more closely spaced ribs. The spine bases are very difficult to discern but the major ones appear to be very long and the minor have been observed on the anterior portions of the ribs only.

The brachial valve is rather strongly concave, particularly in the umbonal region. The auriculations are much more strongly flattened than those of the pedicle valve and the cardinal extremities are rectangular. Well marked concave concentric ribs with abrupt anterior edges are developed. They are much more closely spaced than the ribs of the pedicle valve, there being five to seven ribs per 5 mm. on the median anterior portion of the valve. The arrangement of the spine bases has not been observed, but the whole valve appears to have been covered with fine adpressed spines.

Internal structure: The pedicle valve has very indistinctly defined muscle scars, and the whole interior is crossed by concentric ribs.

The interior of the brachial valve, too, is crossed by strong concentric lamellae. The cardinal process is rounded on its ventral surface except at the posterior extremity where it is slightly bilobed, while its dorsal surface is distinctly trifid. The median septum is small and extends from approximately 1 mm. anterior to the base of the cardinal process, to the anterior limits of the adductor muscle scars, and in some cases slightly beyond. The septum gradually increases in height and is truncated anteriorly. Prominent cardinal ridges arise from the base of the cardinal process and extend to the cardinal extremities. The adductor muscle scars are lacrimate in shape and are slightly raised above the remainder of the shell. No brachial ridges have been observed.

Dimensions.—(All measurements in millimeters.)

Pedicle valves

Length	Width	Length on curvature	Number of ribs per 10 mm.
11	11	16	6
11½	12	18	5
11	11	18	6
12	11	ca. 16	6
12	ca. 11	16	5
11	ca. 10.5	ca. 14	5
9	ca. 9	12	—

Brachial valves

Length	Width	Length of median septum	Length of adductor muscle scars	Number of ribs per 10 mm.
10	10	—	—	5
7	8	—	—	6
13	14	—	—	5
12	13	5	4.5	5
8.5	10	—	—	—
9	11	4	3	5
9	11	4	3	—
10	10	—	—	4
8.5	10	—	—	6
9	11.5	4	3	6
8	7.5	3.5	2.5	6
10	11	—	—	5
6.5	7.5	—	—	6
8	8.5	—	—	6

Remarks.—Dun (1920) referred this form to the lamellibranch *Posidoniella*, though with some doubt. He had at his disposal five specimens, which, from his description, appear to have included both pedicle and brachial valves. He states "they resemble *Athris royssii* to some extent," but "differ in the presence of so few concentric ridges." The present specimens show that the spines do not arise in a fimbriate fashion from the

anterior edge of the concentric ribs as in the athyrids, but rather are apparently developed from spine bases situated on the flattened surfaces of the ribs. The impression of fimbriate lamellae is due to the adpression of the spines during preservation. Moreover, the spines are definitely cylindrical tubes as in other productids, and not flattened as in athyrids.

The present species is closely comparable with *E. elegans* as described by Thomas (1914) in general configuration and in the nature and arrangement of the ribbing, but the latter species has a slightly concave brachial valve and cardinal ridges which are directed anterolaterally from the base of the cardinal process, whilst the former has a rather strongly concave brachial valve and cardinal ridges along the hinge line. Comparison with this and other members of the group is rendered more difficult by the poor preservation of the exterior of the present species due to the relatively coarse nature of the matrix.

From *E. venustus*, *E. subelegans* and *E. eximus* it differs in its smaller size and in the relatively greater width of its concentric ribs, while *E. exquisitus* possesses an entirely different type of concentric ornament. Unfortunately the full internal features of none of these species is available for comparison.

It is worthy of note that the specimen described as *E. elegans* figured by Paeckelmann (1931 pl. 16, fig. 8) has straight cardinal ridges along the hinge line, and has a brachial valve of a convexity similar to *E. gradatus*.

From *E. crameri* it differs in size and arrangement of the concentric ribs. The forms referred to *E. elegans* by Chao (1927), do not appear to be correctly designated, and they differ from *E. gradatus* in the same features as does *E. crameri*. The American species *E. biseriatus* (Hall) as interpreted by Weller (1914) is remarkably similar to *E. gradatus* in all observable details. Hence the closest comparisons are with the *E. elegans* of Paeckelmann (1931) and with the *E. biseriatus* of Weller.

Locality.—This species has so far been found only at the type locality—the hillside at Babbinboon; grid reference 570–637, Attunga One Mile Military Sheet. This locality is near the top of the Lower Burindi Group.

Genus PUSTULA Thomas

Pustula THOMAS, 1914 (in part), Mem. Geol. Surv. Gt. Britain, Palaeont. 1, p. 259 et seq.; pl. 18, fig. 1–6, 10–13; pl. 19, fig. 1–6,15; pl. 20, fig. 1–11.

Pustula Thomas. CHAO, 1927, Paleont. Sinica, (B), vol. 5, no. 2, p. 63.

Pustula Thomas. MUIR-WOOD, 1929, Ann. Mag. Nat. Hist., vol. 5, p. 106.

Pustula Thomas. PAECKELMANN, 1931, Abh. Preuss. Geol. Landesanst. (n.f.), vol. 136, p. 139–151, pl. 13, fig. 2–5; pl. 14, fig. 1–5; pl. 15, fig. 1–6.

Pustula Thomas. SUTTON, 1938, Jour. Paleont., vol. 12, p. 554–5, pl. 66, fig. 8–10.

Genotype.—*Productus pustulosus* (Phillips).

Diagnosis.—See Sutton, 1938; Paeckelmann, 1931.

Range.—In England the earliest certain record of the genus is *P. subpustulosa* from the Z zone, although doubtful representatives of this species have been found as low as Zone B. (Thomas, 1914, p. 280). Other species range to the top of the Viséan.

The lowest horizon on which *Pustula* has been found in Germany appears to be the crinoidal limestone of "Wasserfall vei Velbert" which is Tournaisian-Viséan.

In America several species have been recorded from the lower Tournaisian, e.g., *P. chouteauensis* Branson and *P. echinata* Moore from the Chouteau limestone (Branson, 1938), and *P. praecedens* Stainbrook from the Percha Shale (Stainbrook, 1947). It is known to be represented in the Pennsylvanian by such forms as *P. symmetricus* (McChesney) from the Pottsville formation.

According to Chao (1928, p. 54) "No typical *Pustula* is represented in the survey collections from the Upper Paleozoic formations of China."

PUSTULA ABBOTTI n. sp.
Pl. 49, fig. 4–6

Productus pustulosus Phillips. VOISEY, 1940, Proc. Linnean Soc. N. S. Wales, vol. 65, pts. 1 and 2, p. 199.

Productus cf. *pustulosus* Phillips in Voisey, 1940, p. 199.

Holotype.—F. 1431 University of New England Collections.

Description.—External structure: The shell is of average size for the genus. The

pedicle valve is most strongly convex toward the umbo, which slightly overhangs the hinge line. The auriculations are small and rather sharply defined. The flanks are steep and the median sinus is broad and shallow. The surface is crossed by distinct but irregular concentric ribs, with approximately five ribs per 10 mm. on the median anterior portion of the valve, this number decreasing toward the umbo and the auriculations. The spine bases are elongate (usually several times as long as wide) and are irregularly arranged on the ribs. There are eight to ten spine bases per 5 mm. along each rib.

The brachial valve is slightly concave with a very shallow fold on the anterior portion. The concentric ribs are much less distinct than those of the pedicle valve, and the spine bases are small, either equidimensional or only slightly elongate, and arranged in irregular rows.

Internal structure: The muscle scars of the pedicle valve are indistinguishable. The surface is crossed by concentric ridges corresponding with the depressions of the external surface, and between the ridges are depressions corresponding in position with the spine bases.

The brachial valve bears a strong cardinal process with a strongly bifid posteroventral and trifid dorsal surface. Strong ridges arise from the base of the cardinal process and parallel the length of the hinge. The median septum is broad and high posteriorly but gradually decreases anteriorly, and is approximately three fifths as long as the valve. The surface is crossed by fine ridges which become more widely separated anteriorly, and the anterior and anterolateral portions bear linearly arranged fine sharp spines between the ridges. The adductor scars are long and narrow, being two-fifths as long as the valve. No dendritic markings have been observed on the scars.

Dimensions.—(All measurements given in millimeters)

Pedicle valves

Length	Width	Width at hinge
33±	36±	—
30±	30±	25
30±	32±	—

Brachial Valves

Length	Width	Length of median septum	Length of adductor field	Width of adductor field
26	32	14	10	4
24	—	14	9.5	3.5
24	32	—	—	—
23	28	—	—	—
—	—	13+	8.5	4.5

Remarks.—Of overseas species, *P. subpustulosa* Thomas appears to be most closely related morphologically to this species but the former has slightly broader ribs and coarser spine bases as well as smaller length/width ratios. *P. subpustulosa* occurs chiefly from zone K to horizon γ in the British region. There appear to be no other closely comparable species.

The specimens from L. 71 which I have assigned to this species are for the most part distorted, and a few of them are much larger than any from the type locality. However specimens of comparable size from the two localities are indistinguishable in all observable characters.

Localities.—The type locality is the railway cutting near Nooroo, West of Stroud; grid reference 903–985 Dungog One Mile Military Sheet, (L. 54 University of New England Collections).

It has also been found on the Barrington-Rawdon Vale Road: grid reference 913–371, Gloucester One Mile Military Sheet, L. 71; (see Voisey 1940, p. 199).

Horizon.—Probably upper Tournaisian. Both localities are within the upper half of the Lower Burindi Group.

PUSTULA GRACILIS n. sp.
Pl. 49, fig. 1–3

Holotype.—F. 1447 University of New England Collection.

Description.—External structure: The

shell is of the medium size for the genus and is slightly wider than long. The pedicle valve is not strongly convex. The hinge line is slightly shorter than the maximum width of the shell. The auriculations are rather broad and gradually merge into the body of the valve. The flanks are not steep (ca. 45°). A median flattening is developed in most specimens, but in others the venter is evenly rounded. The surface is crossed by numerous vaguely defined, irregular concentric ribs, there being seven to nine ribs per 10 mm. on the median anterior portion of the adult valves. The spine bases are elongate, in most cases completely crossing the ribs, and spaced at approximately eight per 5 mm. on the anterior portion of the valve. In some specimens there is a tendency to reduce the strength of the ribs toward the umbo and the spines assume a very roughly quincuncial pattern. The spines themselves are very slender and are adpressed.

The brachial valve is markedly concave, leaving a very thin visceral region. The umbo is strongly concave, and the umbonal angle is approximately 100°. The auriculations are broad and flat. The concentric ribbing is much less distinct than on the pedicle valve, and the ribs are more closely spaced (12 to 16 per 10 mm. on the anterior portion of the valve). The spine bases are only slightly elongated, are very roughly simi-quincuncial in arrangment and there are eight or nine per 5 mm. on each rib. The spines are finer than those of the pedicle valve.

Internal structure: The adductor scars of the pedicle valve are very indefinite, and the divaricator scars are not visible in any of the specimens examined. The whole inner surface is crossed by concentric markings which bear depressions corresponding in position with the spines of the exterior.

The brachial valve has strong cardinal ridges arising from the base of the cardinal process and becoming progressively weaker toward the cardinal extremities. The cardinal process is bifid on its posteroventral surface. Its dorsal surface bears a long, deep and very narrow median groove, and each half is then subdivided by a shorter groove. The median septum is short (less than half the length of the valve) and slight, gradually decreasing in height anteriorly. The adductor scars are slightly elevated and broadest toward their anterior extremities, imparting a strong subtriangular outline. No dendritic markings have been observed on the muscle scars.

Dimensions.—(All measurements in millimeters)

Pedicle valves

Length	Width	Width at hinge
30	33	27
25	31	25

Brachial valves

Length	Width	Width at hinge	Length of median septum	Length of adductor scars	Width of adductor scars
28	40	34	10	5.5	7
26	37	—	—	—	—
25	38±	—	—	—	—
25	38	28	10	5.5	5
28	38	—	14	7.5	7±
—	36±	—	9.5	5.5	5
25	38±	—	11	5.5	5
19	27	24±	6.5	—	—
16	20±	18±	—	—	—

Remarks.—This species is readily distinguished from *P. abbotti*, n. sp., by its stronger pedicle spine bases which are more nearly semiquincuncially arranged; the coarser spine bases of the brachial valve; the relatively shorter median septum in the brachial valve; the relatively shorter, broader and much more triangular brachial adductor scars.

It does not appear to be closely comparable with any overseas species with which I am acquainted.

Locality.—Two hundred yards upstream from Cameron's Bridge, Rouchel Brook, in Pors. 1 and 34, Par. Rouchel, Co. Durham. This is the only locality from which the species is known.

Horizon.—As mapped by Osborne (1950, p. 42) it is 800–1000 feet above the base of the Lower Kuttung Group. It is probably basal Viséan in age.

Genus LINOPRODUCTUS Chao

Linoproductus CHAO, 1927 (in part), Paleont. Sinica (B), vol. 5, no. 2; p. 128–139, p. 140–146; pl. IV, fig. 17; pl. XI, fig. 7–10; pl. XIII, fig. 1–7,17–18; pl. XIV, fig. 1–12; pl. XV, fig. 25–27.

Linoproductus Chao. MUIR-WOOD, 1929 (in part), Ann. Mag. Nat. Hist., vol. 5, p. 105.

Linoproductus Chao. PAECKELMANN, 1931, Abh. Preuss. Geol. Landesanst. (n. f.), vol. 136, p. 206–230; pl. 19, fig. 1–10; pl. 20, fig. 1–7; pl. 21, fig. 1–4.

Linoproductus Chao. SUTTON, 1938, Jour. Paleont. vol. 12, p. 557–8; pl. 65, fig. 8–14.

Linoproductus Chao. PRENDERGAST, 1943, Jour. Roy. Soc. West. Aust., vol. 28, p. 20–25, pl. 3, fig. 1–5.

Diagnosis.—See Chao, 1927, p. 128; Prendergast, 1943, p. 20.

Range.—In Great Britain the genus is represented only rarely before the Viséan but it is abundant in rocks of that age. In Germany, Paeckelmann records it from rocks of Viséan age or younger, Delepine (1928, pp. 27–29) records species referable to the genus from as low as the K_2 zone in Belgium. In China the genus does not appear to occur below the Viséan, while in America it is known to range from the base of the Lower Carboniferous.

Of course it ranges into the Upper Carboniferous and Permian in all continents.

Linoproductus sp.
Pl. 49, figs. 11–13

Description.—External structure: This species is small, very thin shelled, and rather fragile, and is thus almost always distorted. The pedicle valve is more or less ovate in outline, the hinge line being very short. The umbo is small and blunt and does not appear to overhang the hinge line. Auriculations are very small but are sharply separated from the body of the valve. No sinus is present, the valve being evenly rounded across the venter. The flanks are steep. The costae which increase by intercalation, are very fine, ranging between 15 and 20 per 5 mm. on the median anterior portion of the valve. They may become slightly irregular anteriorly. Concentric ribs are present, being best developed on the posterior half of the valve and becoming broader and less well defined on the anterior half. No spines have been observed.

The brachial valve is similar in outline to the pedicle valve and follows its contour rather closely leaving only a very thin visceral region. It does not appear to be geniculate. The umbo is small and slightly concave. The costae are of the same type and number as those of the pedicle valve, but they increase both by intercalation and bifurcation. The concentric ribs are similar to those of the pedicle valve.

Internal structure: The pedicle valve is unthickened toward the umbo. The muscle scars are obscured by the costation.

The brachial interior bears a very fine low median septum which is approximately one third the length of the valve. Low cardinal ridges are developed along the hinge line. The cardinal process is short and appears to be slightly bifid ventrally. Its dorsal surface has not been seen.

Remarks.—The material upon which this description is based is all somewhat distorted and is all in the form of moulds, but it is so distinctive that it warrants description.

The specimens from L. 35 have distinctly stronger and more numerous wrinkles on both the pedicle and brachial valves, and may be specifically distinct from the specimens from L. 55, but insufficient material is available to be certain of this.

Linoproductus sp. is similar to *L. tenuistriatus* (Verneuil) as described by Chao (1927), in its narrow hinge, outline, and the absence of spines but it has finer costae and apparently a smaller and less protruding umbo. Paeckelmann (1930, pl. 21, fig. 1) figures a form which he refers to a new species *L. rhenanus*, which is similar to the form described herein in its narrow hinge, lack of spines and small umbo, but differs in its coarser ornament and thicker shell. The American Lower Carboniferous forms, which are usually referred to *L. ovatus* (Hall) (e.g., Weller, 1914), all have much coarser ornament than the present species.

Localities.—Hillside at Babbinboon, grid reference 570–637, Attunga One Mile Military Sheet (L. 35 University of New England Collections); and the railway cutting at Nooroo, grid reference 903–985, Dungog One Mile Military Sheet (L. 55 University of New England Collections). Both of these localities are within the lower Burindi group.

REFERENCES

BENSON, W. N., & DUN, W. S., 1920, The geology of the Great Serpentine Belt of N. S. W. Part IX, Section B: Proc. Linnean Soc. New South Wales, vol. 45, no. 179, p. 337–374.

BRANSON, E. B., et al., 1938, Stratigraphy and paleontology of the Lower Mississippian of Missouri: Univ. of Missouri Studies, vol. 13, no. 3, 208 p., 20 pl.

CAREY, S. W., & BROWNE, W. R., 1938, Review of the Carboniferous stratigraphy, tectonics and palaeogeography of New South Wales and Queensland: Jour. Proc. Royal Soc. New South Wales, vol. 72, p. 591–614.

CHAO, Y. T., 1927, Productidae of China, I, Producti: Paleont. Sinica (B), vol. 5, no. 2, 192 p., 26 pl.

COOPER, G. A. 1944, *in* Shimer, H. W., & Shrock, R. R., 1944, Index fossils of North America: Chapman and Hall, London.

DELEPINE, G., 1928, Les brachiopodes du marbre noir de Dinant: Mus. Roy. Hist. Nat. Belgique, mém. 37, p. 1–38, 6 pl.

DUN, W. S., 1902, Notes on some Carboniferous brachiopods from Clarencetown: Records Geol. Surv. New South Wales, vol. 7, no. 1, p. 72–88, pl. 21–23.

——, 1902, Description of a new species of *Productus* from the Carboniferous System of New South Wales: Records Geol. Surv. New South Wales, vol. 7, no. 1, p. 91–93, pl. 25.

ETHERIDGE, R., JR., 1878, Catalogue of Australian fossils: London.

IVANOV, A. P., 1935, Brachiopoda of the Middle and Upper Carboniferous of the Moscow Basin: Trans. Geol. Trust,. Fasc. 8, p. 1–163.

KING, R. H., 1938, New Chonetidae and Productidae from Pennsylvanian and Permian strata of north-central Texas: Jour. Paleont., vol. 12, no. 3, p. 257–279, pl. 36–39.

KONINCK, L. G. DE, 1876–77, Descriptions of the Palaeozoic fossils of New South Wales: Reprinted as Memoir 6, Paleontology, Geol. Surv. New South Wales.

LAUDON, L. R., 1948, Osage-Meramec contact: Jour. Geol., vol. 56, no. 4, p. 288–302.

MUIR-WOOD, H. M., 1929, The classification of the British Carboniferous brachiopod subfamily Productinae: Ann. Mag. Nat. Hist., vol. 5, p. 100–108.

——, 1948, Systematic descriptions of Brachiopoda, *in* Malayan Lower Carboniferous fossils: British Museum (Natural History), p. 24–77, 10 pl.

——, 1951, The proposed use of the plenary powers to validate the trivial names of two nominal species of the class Anthozoa, and of eight nominal species of the class Brachiopoda published by William Martin in 1809 in the work entitled Petrificata Derbiensia and matters incidental thereto: Bull. Zool. Nomen., vol. 1, p. 7–32.

NALIVKIN, D., 1937, Brachiopods of the Upper and Middle Devonian and Lower Carboniferous of north-eastern Kazakhstan: Trans. Centr. Geol. Prosp. Inst. Moscow, vol. 99, p. 1–200, 39 pl.

OSBORNE, G. D., 1922, The geology and petrography of the Clarencetown-Patterson District. Part I: Proc. Linnean Soc. New South Wales, vol. 47, p. 161–198.

——, 1950, The structural evolution of the Hunter-Manning-Myall Province, New South Wales: Monograph 1, Royal Soc. New South Wales.

PAECKELMANN, W., 1931, Die Fauna des deutschen Unterkarbons, II: Abh. Preuss. Geol. Landesanst., (n.f.), vol. 136, p. 1–440, 41 pl.

PRENDERGAST, K. L., 1943, Permian Productinae and Strophalosiinae of Western Australia: Jour. Royal Soc. W. Australia, vol. 28, p. 1–62, 6 pl.

STAINBROOK, M. A., 1947, Brachiopoda of the Percha shale of New Mexico and Arizona: Jour. Paleont., vol. 21, no. 4, p. 279–328, 4 pl.

SUTTON, A. H., 1938, Taxonomy of Mississippian Productidae: Jour. Paleont., vol. 12, p. 537–569, 5 pl.

——, & SUMMERSON, C. H., 1943, Cardinal Process of Productidae: Jour. Paleont., vol. 17, no. 4, p. 323–330, 2 pl.

THOMAS, I., 1914, The British Carboniferous Producti, I. Genera *Pustula* and *Overtonia:* Mem. Geol. Surv. Great Britain, Palaeontology, vol. 1, no. 4, p. 197–366, pl. 17–20.

TSCHERNYSHEW, T., 1902, Die Obercarbonischen Brachiopoden des Ural und des Timan: Mem. Com. Geol. St. Petersberg, vol. 16, no. 2, p. 1–749, 63 pl.

VOISEY, A. H., 1940, The Upper Palaeozoic rocks in the country between the Manning and Karuah Rivers, New South Wales: Proc. Linnean Soc. New South Wales, vol. 65, pts. 1–2, p. 192–210.

——, 1945, Correlation of some Carboniferous sections in New South Wales: Proc. Linnean Soc. New South Wales, vol. 70, pts. 1–2, p. 34–40.

WELLER, J. M., et al., 1948, Correlation of the Mississippian formations of North America: Geol. Soc. Am. Bull., vol. 59, p. 91–196.

WELLER, S., 1914, Mississippian Brachiopoda of the Mississippi Valley basin: Illinois Geol. Surv. Monograph 1, p. 1–508, 83 pl.

MANUSCRIPT RECEIVED APRIL 1, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 481–491, PL. 51, 52, MAY 1956

EARLY ORDOVICIAN NAUTILOIDS FROM VIRGINIA*

A. G. UNKLESBAY AND ROBERT S. YOUNG
University of Missouri and Virginia Division of Geology

ABSTRACT—The Chepultepec-Stonehenge transition unit in Virginia has yielded a nautiloid fauna consisting of 17 species divided among 10 genera. Of these species four are known from the Gasconade of Missouri, three from the Tanyard of Texas, two from the Chepultepec of Alabama and Tennessee, two from the Oneota of Wisconsin, one from the Smithville of Arkansas, and one from the Upper Ozarkian of Pennsylvania. Two new genera *Anguloceras* and *Chepuloceras* are established. New species described are: *Anguloceras ovatum* (type species), *A. depressum*, *A. rotundum*, *Woosteroceras chepultepecense*, *Pachendoceras brevicameratum*, *P. parvum*, and *Chepuloceras inelegans* (type species). The age of the beds yielding this fauna is not definitely known, but it is almost certainly Gasconadian.

INTRODUCTION

RECENT studies in the Ordovician of Virginia have revealed the presence of silicified fossils in the Chepultepec-Stonehenge transition interval between the Conococheague formation (Cambrian) and beds of Nittany age (Ordovician). The fossils present are nautiloids, brachiopods, and gastropods, in order of abundance. They are restricted to thin beds and are sporadic within these beds. The faunas are not well mixed, i.e. the gastropods and nautiloids occur together, but are not associated with the brachiopods. In addition to the forms described here these beds have yielded *Ophileta* sp., *Sinuopea* sp., *Tetralobula delicatula*, *Findelnburgia buttsi*, and two or three other species of *Finkelnburgia*.

The nautiloids from these beds comprise an assemblage of 17 species divided among 10 genera. Two genera and seven species are new. Of the previously known species four are also known from the Gasconade of Missouri, three from the Tanyard of Texas, two from the Oneota of Wisconsin, one from the Smithville of Arkansas, and one from an Upper Ozarkian horizon in Pennsylvania. The genus *Shelbyoceras*, previously known from the Upper Cambrian of Missouri, is questionably represented in this assemblage.

In addition many of the fragmental specimens seem to be close to other Gasconade and Tanyard species but cannot be placed with certainty. On the basis of the nautiloid fauna it seems that these beds can be more closely correlated with the Gasconade and Tanyard than with other parts of the Ordovician column. However, the small size and generally primitive character of the nautiloids suggest that their environment was not particularly conducive to the development of a healthy and varied fauna. Also the presence of *Shelbyoceras*-like forms, and of *Clelandoceras*, suggests that these sediments might actually represent a longer period of time than the Gasconade and Tanyard beds.

The materials for this study were prepared in the laboratories of the Virginia Division of Geology, and the field expenses were defrayed in part by a research grant from the Virginia Academy of Science. The systematic paleontology was completed by the senior author as a summer Research Fellow sponsored by the University of Missouri Research Council.

STRATIGRAPHY

The fossils described in this paper were collected from a 400–500 foot limestone series, gradational with impure limestones and dolomites of the underlying Conococheague (Cambrian) and with tan dolomites of the overlying Beekmantown (Ordovician). This section consists mostly of medium- to dark-gray, medium-grained limestone which weathers characteristically white. Most of the beds are massive and thick-bedded though some are faintly laminated with buff argillaceous layers. The precise age of this limestone section is somewhat problematic, although it is generally considered basal Ordovician. In the

* Published with the permission of the State Geologist of Virginia.

past, the terms "Beekmantown," "Stonehenge," and "Chepultepec" have been applied. More recently, only Stonehenge and Chepultepec have been given consideration. Whether either of these terms is wholly applicable has not yet been demonstrated.

The following brief history of the origin and extension of the terms Chepultepec and Stonehenge perhaps will reveal the reasons for stratigraphic uncertainty in this part of the Virginia Paleozoic section.

Chepultepec formation.—The Chepultepec was named by Ulrich (1911, p. 638) for exposures near Chepultepec (now Allgood), Blount County, Alabama. No detailed section is given; however, Ulrich's description indicates that the basal Chepultepec contact is concealed within a 300–400 foot interval, and that the top is bounded by a disconformity. The Chepultepec is described as cherty magnesian limestone, although it is referred to, within the text, as the "Chepultepec chert formation," "Chepultepec formation," and "Chepultepec limestone."

Fossils are most common in the upper part of the unit; about 20 species were collected by Ulrich at the type locality.

The following is a partial faunal list, as cited by Ulrich (1911, p. 639):

Archeocyathus?
Scenella
Helicotoma uniangulatum (Hall)
Holopea? turgida Hall
Sinuopea sweeti (? Whitfield)
Piloceras newton-winchelli Ruedemann
Cameroceras
Orthoceras

Tentative correlations, on a faunal basis, were proposed with (1) the Gasconade of Missouri, (2) "a cherty dolomite near Roaring Spring, Pennsylvania," (3) the top of the Little Falls dolomite at Little Falls and Whitehall, N. Y., and (4) the upper Oneota dolomite in Wisconsin, Iowa, and Minneosota.

Ulrich states (1911, p. 638), "So far as known, it [Chepultepec formation] represents the last of Ozarkian deposits in this province [the Appalachian Valley region]."

The term "Chepultepec" has been extended northeastward to Tennessee (Oder, 1934; Rodgers, 1953; and others), southwestern Virginia (Butts, 1933, 1940; Miller and Fuller, 1954), and northern Virginia (Butts, 1933, 1940; Edmundson, 1945). With one exception, the cited authors propose a basal Ordovician age for the Chepultepec; Oder (1934) believes that the Chepultepec is uppermost Cambrian, recognizing the Stonehenge limestone as basal Canadian.

Stonehenge member, Beekmantown group.—The Stonehenge was named for exposures near Stonehenge, Franklin County, Pennsylvania (Stose, 1908, p. 703–704), and was described thus:

> Near the base [of the Beekmantown] are siliceous banded beds and large "edgewise" conglomerate closely resembling the Conococheague formation. These have been separated as a transition phase under the name Stonehenge member of the Beekmantown.

Upper and lower contacts of the Stonehenge are gradational, and a two-fold division within the member is indicated by a measured section, located one mile east of Chambersburg, Pennsylvania. That part of this section allotted to the Stonehenge is described by Stose (1908, p. 704) as:

215 feet. Fine-grained light- to dark-gray limestone containing contorted laminae of sandy matter, that stand in relief or fall to sandy shale on weathering, and thick beds of "edgewise" conglomerate. Contain Gasteropods in upper portion and fine fragments of Trilobites in lower part.

260 feet. Dark- to light-gray limestone, with sandy laminae less developed than in overlying beds. Contain *Orthis, Ophileta* and Trilobite fragments.

The two-fold division of the Stonehenge has been recognized by other workers in Pennsylvania and Maryland (Bassler, 1919; Wilson, 1952); however, the junior author has been unable to differentiate these units in northern Virginia.

Bassler and Butts extended usage of Stonehenge into Maryland and Virginia. Butts (1933) mapped the Stonehenge and Chepultepec as a unit, but indicated overlap of the Chepultepec (Ozarkian) by the Stonehenge (Canadian).

Current usage: In the past 20 years Appalachian stratigraphers have begun to overcome the barrier set up by Ulrich's original concept of the Chepultepec as Ozarkian and the Stonehenge as Canadian. Butts (1940, p. 101) states that

The occurrence of several common species in the Chepultepec, Stonehenge, and Tribes Hill of New York has led some geologists to the tentative conclusion that these formations are all the same.

Woodward (1951, p. 67–69) ably reviews the Chepultepec-Stonehenge problem, and arrives at the following conclusions regarding application of these terms in the central Appalachians:

> The major elements of the correlations . . . suggest that the Stonehenge—upper Chepultepec—Tribes Hill constitute a single stratigraphic horizon, while the Larke—lower Chepultepec—upper Little Falls—Gasconade—Oneota also constitute a stratigraphic horizon, perhaps slightly older than the former. In other words, the Chepultepec limestone of Alabama—Tennessee—Virginia may also include horizons slightly older than those of the Stonehenge limestone of Pennsylvania—Maryland—West Virginia with which, however, it is still partly contemporaneous. These slight differences of level still further document the wisdom of using the joint name Chepultepec-Stonehenge until more adequate data have been discovered and interpreted.

It is interesting to note that the most recent, authoritative correlation chart of the Ordovician (Twenhofel et al., 1954) indicates essential time equivalence for the Chepultepec of Roanoke Valley, Virginia, and the Stonehenge of southern Pennsylvania and Maryland. Only the term "Beekmantown" is cited for use in the intervening area.

In view of uncertainty of the stratigraphic position of beds from which the cephalopods described herein were collected, the junior author prefers the terminology of Woodward (1951, p. 59). Therefore, the dual term "Chepultepec-Stonehenge" is used herein for the 400–500 foot transitional unit between definite Cambrian (Conococheague) and Ordovician (Nittany equivalent).

Specific localities.—Locality 1. Strasburg, Virginia, quadrangle; 2.7 miles N. 12°E. of the center of Woodstock (Edinburg quadrangle), and 1.7 miles S. 69°W. of Maurertown (Strasburg quadrangle). Fossil-bearing outcrops of the Chepultepec-Stonehenge are abundant along the east side of Pughs Run. The Chepultepec-Stonehenge sequence at this locality is involved in tight folding; fracture cleavage is well developed in the limestones. The beds at this locality are unusually high in carbonaceous matter. Fossils in this particular area may be deformed. Collection made at approximately the middle of the unit.

Locality 2. Roanoke, Virginia, quadrangle; in an abandoned quarry on the east side of Carvin Creek, 0.6 mile N. 64°W. of the confluence of Carvin and Tinker creeks. The quarry is approximately 3.5 miles north of the center of Roanoke. Because of poor exposures, the collection cannot be accurately located with respect to formational limits, although lithologic comparisons indicate that the quarry is in lower Chepultepec-Stonehenge.

SYSTEMATIC DESCRIPTIONS

Altogether more than 200 fragmental nautiloids have been recovered by dissolving the fossil-bearing limestone in acid. However, only a few of these are identifiable with any degree of certainty. They are all small, relatively simple, straight or slightly curved forms with very closely spaced septa. Only the phragmocones are preserved and none possesses a living chamber. Many of the specimens are distorted so that the septa and siphuncles are squeezed out of normal position. However, the distortion is not so extreme but that the original nature of the shell can be ascertained.

Order ELLESMEROCERATIDA Flower
Family ELLESMEROCERATIDAE Kobayashi
Genus SHELBYOCERAS Ulrich & Foerste, 1931
SHELBYOCERAS cf. S. BESSEMERENSE Ulrich, Foerste, & Miller
Pl. 51, fig. 2

The specific affinities of one fragmentary specimen in this collection are not clear but the specimen seems very close to *S. bessemerense* as described by Ulrich, Foerste, and Miller. This specimen is 9 mm. long, and near its mid-length it is 5.2 mm. high and 3.4 mm. wide. It is septate throughout and slightly curved endogastrically. The cross section is oval, being compressed laterally and slightly more narrowly rounded dorsally than ventrally. The camerae are very short, about one-half millimeter; the sutures are nearly straight and slope apicad from the venter to the dorsum. The siphuncle is ventral but not marginal in position and is less

than 1 mm. in diameter. It is nearly circular in cross section.

Occurrence.—Locality 1.

Repository.—Univ. Mo. 12711.

SHELBYOCERAS sp.
Pl. 51, fig. 1

One specimen in this collection seems to have the generic characteristics of *Shelbyoceras*, but is not very close to any previously described species. Because of its poor preservation it is inadequate to justify a new species. This specimen is septate throughout, and the septa are very closely spaced. It is slightly curved endogastrically and expands rapidly, particularly in the orad portion. The cross section is oval, with the greatest width being near the dorsal side. Both the dorsum and venter are subangular with the venter being more acute. The length is 18 mm., and the height increases from 7 mm. at the adapical end to 13 mm. at the adoral end. In the same length the width increases from 4 mm. to 9 mm.

The siphuncle is moderate in size, and is compressed to an elliptical cross-section. At the adapical end it is 1 mm. high and 0.7 mm. wide. At the adoral end it is 1.2 mm. wide and 2.1 mm. high. At the adapical end it is near to but not in contact with the venter. At the adoral end the siphuncle is displaced to a position to the left of a median position.

Remarks.—This specimen somewhat resembles *S. buttsi* Ulrich, Foerste, and Miller, but that species is rapidly expanded only in the living chamber.

Occurrence.—Locality 1.

Repository.—Univ. Mo. 12712.

Genus LEVISOCERAS Foerste, 1925
LEVISOCERAS ELLIPTICUM Ulrich
Foerste, & Miller
Pl. 51, fig. 3,4

Levisoceras ellipticum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. Am., Special Paper 49, p. 138, pl. 63, fig. 7–13.

Levisoceras ellipticum UNKLESBAY, 1954, Jour. Paleont., vol. 28, p. 650, pl. 70, fig. 3–7.

Three small specimens of this species have been found in the Roanoke quarry and one is from near Woodstock. All are septate throughout. They are rather strongly curved endogastrically, and are ellipitcal in cross-section, being compressed laterally. At the adoral end of the best specimen the conch is 3.5 mm. wide and 4.8 mm. high.

EXPLANATION OF PLATE 51

All figures are ×2

FIG. *1*—*Shelbyoceras* sp. Lateral view with ventral side to the left. Univ. Mo. 12712. (p. 484)

2—*Shelbyoceras* cf. *S. bessemerense* Ulrich, Foerste, & Miller. Lateral view with ventral side to the right. Univ. Mo. 12711. (p. 483)

3,4—*Levisoceras ellipticum* Ulrich, Foerste, & Miller, Ventral and lateral views. Univ. Mo. 12713. (p. 484)

5,6—*Levisoceras instabile* Ulrich, Foerste, & Miller. Lateral views of two small specimens, Univ. Mo. 12714, 12731. (p. 485)

7—*Levisoceras transitum* Ulrich, Foerste, & Miller. Lateral view with ventral side to the right. Univ. Mo. 12715 (p. 485)

8—*Ectenoceras chepultepecense* Ulrich, Foerste, & Miller. Lateral view with ventral side to the left. Univ. Mo. 12716. (p. 486)

9–14—*Ectenoceras compressum* Ulrich, Foerste, & Miller. Lateral views *9,10,13,14;* dorsal view, *11;* septal view *12;* representing six specimens, Univ. Mo. 12717. (p. 486)

15,16—*Ectenoceras exile* Ulrich, Foerste, & Miller. Lateral views of two specimens. Univ. Mo. 12719, 12720. (p. 486)

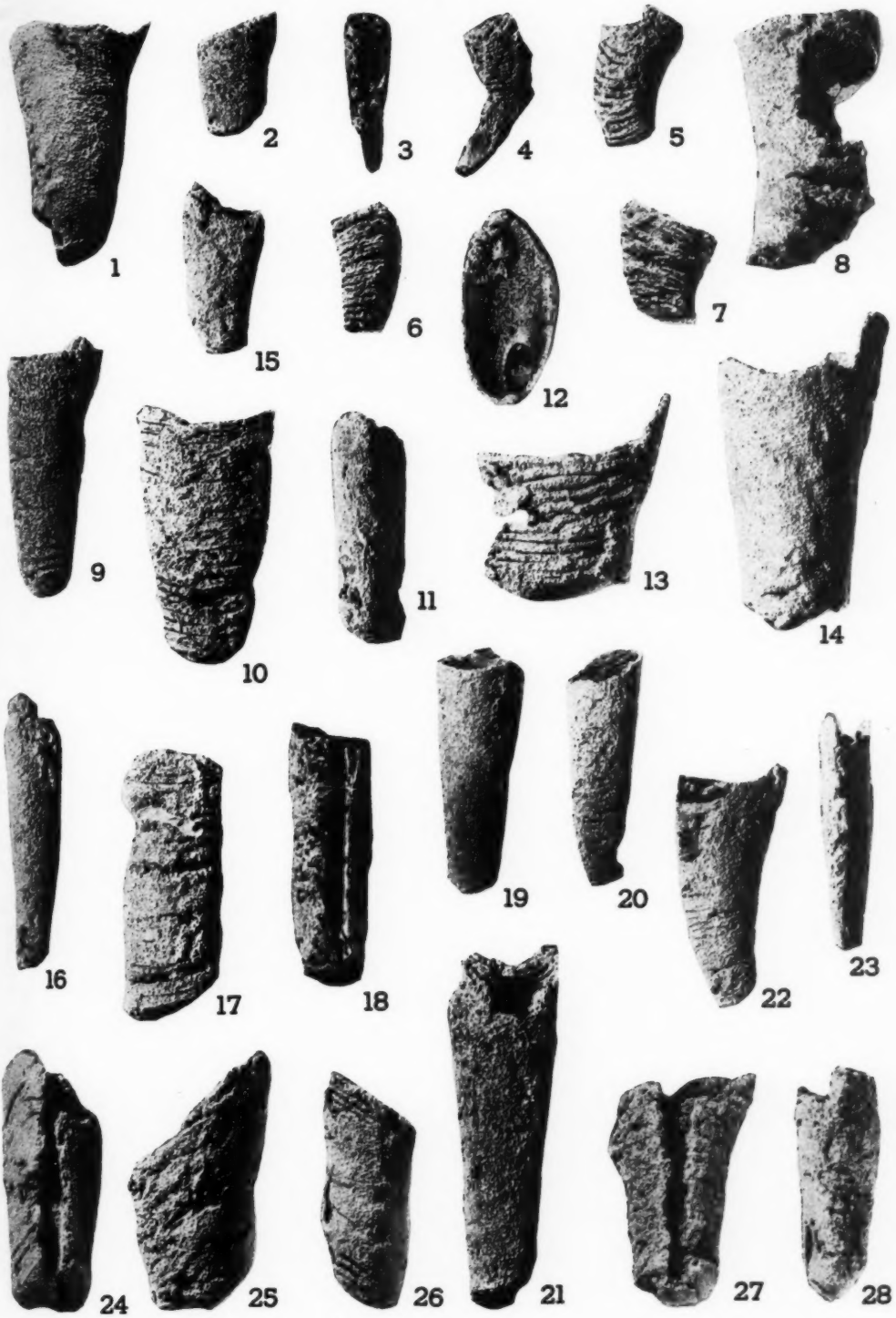
17,18—*Ectenoceras longum* Ulrich, Foerste, & Miller. Lateral and ventral views of one specimen. In *17* the ventral side is to the right. Univ. Mo. 12721. (p. 487)

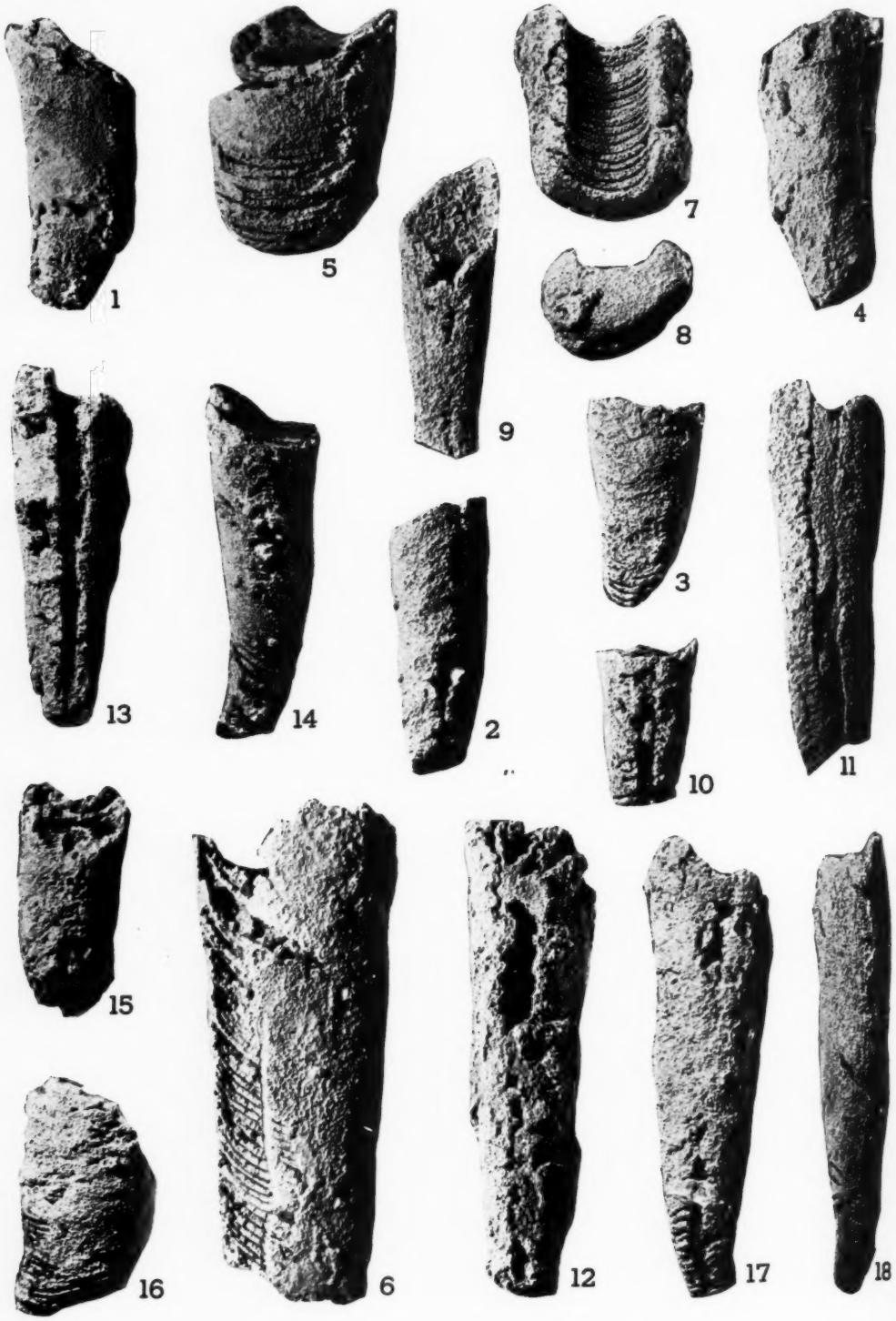
19–21—*Albertoceras staufferi* Ulrich, Foerste, Miller, & Unklesbay. Lateral views of three specimens. In *19* and *20* the ventral side is to the right; in *21*, it is to the left. Univ. Mo. 12722. (p. 487)

22,23—*Clelandoceras elongatum* Ulrich, Foerste, Miller, & Unklesbay. Lateral and dorsal views of one of the best preserved of several specimens. Univ. Mo. 12724. (p. 487)

24–26—*Anguloceras ovatum*, n. sp. Ventral and lateral views of the holotype and a lateral view of a paratype. Univ. Mo. 12726, 12727. (p. 488)

27,28—*Anguloceras depressum*, n. sp. Ventral and lateral views of the holotype. Univ. Mo. 12728. (p. 488)


1
2
3
4
5
8
15
6
12
7
9
10
11
13
14
16
17
18
19
20
22
23
24
25
26
21
27
28


1
5
7
4
8
9
13
14
3
2
11
10
15
16
6
12
17
18

The septa are closely spaced, there being five in a length of 1 mm. They are not strongly curved. The sutures form broad shallow lateral lobes, moderately high dorsal saddles, and low ventral saddles. The siphuncle is large; approximately one-third of the shell height. It is near to but not in contact with the ventral wall. The nature of the septal necks cannot be determined with certainty but they appear to have been short and slightly curved.

Remarks.—Although these specimens are rather poorly preserved their specific affinities seem certain.

Occurrence.—Localities 1 and 2. This species is also known from the Upper Ozarkian of Pennsylvania, the Oneota of Wisconsin and the Tanyard of Texas.

Repository.—Univ. Mo. 12713.

LEVISOCERAS INSTABILE Ulrich, Foerste & Miller
Pl. 51, fig. 5,6

Levisoceras instabile ULRICH, FOERSTE & MILLER, 1943, Geol. Soc. Am., Special Paper 49, p. 138–139, pl. 64, fig. 1–6.

Two small specimens in the Chepultepec collection seem to represent this species. The better one is completely septate, curved endogastrically, and is broadly oval in cross-section. The ventral profile is more narrowly rounded than the dorsal. The specimen is about 10.5 mm. long. At the adoral end it is 4.6 mm. wide and 6.2 mm. high.

The camerae are short, about two and a half make up a length of 1 mm. The sutures form shallow lateral lobes, and low ventral and dorsal saddles. The siphuncle is close to the ventral wall. It is compressed laterally, and its height is slightly less than one-third the height of the shell. The structure of the siphuncle cannot be determined. The other specimen is very similar except it is less well preserved.

Remarks.—This species can be separated from *L. ellipticum* on the basis of its more widely spaced septa and slightly smaller siphuncle.

Occurrence.—Locality 1 and Locality 2. This species is also known from the Gasconade of Missouri, the Oneota of Wisconsin, and the Chepultepec of Alabama and Tennessee.

Repository.—Univ. Mo. 12714, 12731.

LEVISOCERAS TRANSITUM Ulrich, Foerste, & Miller
Pl. 51, fig. 7

Levisoceras transitum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. Am., Special Paper 49, p. 141–142, pl. 65, fig. 4,5.

The specimen here referred to this species is smaller than the holotype and is less flattened on the lateral zones, but in general physiognomy it appears to be a small representative of this species. This specimen is septate throughout, is curved endogastrically, and expands orad rather rapidly. It is 7.5 mm. long, and at the adoral end the height and width are 7.7 and 4.7 mm., respectively.

The septa are exceedingly shallow and slope orad from the ventral to the dorsal side. The sutures form very slight lateral lobes and moderately high dorsal saddles. The siphuncle is ventral in position, and at

---

EXPLANATION OF PLATE 52

All figures are ×2

FIG. *1–4—Woosteroceras chepultepecense*, n. sp. Lateral and ventral views of one syntype 1, 2, and lateral views of two other syntypes 3, 4. Univ. Mo. 12730. (p. 489)

5,6—Pachendoceras brevicameratum, n. sp. Lateral view of a septate specimen (*5*), and a lateral view of the holotype (*6*), Univ. Mo. 11735, and 12734 (holotype). (p. 489)

7,8—Pachendoceras confertum Ulrich, Foerste, Miller, & Unklesbay. Ventral and septal views of the largest of three specimens in this collection. Univ. Mo. 12732. (p. 489)

9–12—Pachendoceras parvum, n. sp. Ventral views of four syntypes. Univ. Mo. 12736. (p. 490)

13,14—Anguloceras rotundum, n. sp. Ventral and lateral views of holotype. Univ. Mo. 12729. (p. 488)

15,16—Bassleroceras cf. *B. bridgei* Ulrich, Foerste, Miller, & Unklesbay. Ventral and lateral views of a septate specimen. Univ. Mo. 12737. (p. 490)

17,18—Chepuloceras inelegans, n. sp. Ventral and lateral views of the holotype. In *18* the ventral side is to the right. Univ. Mo. 12738. (p. 490)

the adoral end of the specimen it is approximately 1.0 mm. in diameter.

Remarks.—Despite the difference in size between this specimen and the holotype, they seem conspecific, and this one appears to represent an earlier part of the shell. The holotype is also from the Chepultepec formation.

Occurrence.—Locality. This species is also reported from the Chepultepec of Tennessee.

Repository.—Univ. Mo. 12715.

Genus ECTENOCERAS Ulrich & Foerste, 1936

ECTENOCERAS CHEPULTEPECENSE Ulrich Foerste, & Miller

Pl. 51, fig. 8

Ectenoceras chepultepecense ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. Am., Special Paper 49, p. 118–119, pl. 58, fig. 6,7.

This species is represented in the Chepultepec collection by one fragmentary slightly distorted specimen which represents only part of a phragmocone. It is distinctly curved endogastrically and is elliptical in cross-section being compressed laterally. The curvature is greater in the adapical portion with a clear tendency to become straight in the adoral portion. This specimen is 10.5 mm. high and 7.0 mm. wide.

The septa are shallow, and closely spaced; there being five of them in a length of 3 mm. The sutures are directly transverse and form only slight lateral lobes and dorsal and ventral saddles. The siphuncle is ventral and marginal in position. It is compressed laterally to an elliptical cross section and at the adoral end of the specimen is about 2 mm. high.

Remarks.—Despite the poor preservation of this specimen its significant characteristics are clearly shown.

Occurrence.—Locality 1. The holotype of this species is from the Chepultepec of Blount County, Alabama.

Repository.—Univ. Mo. 12716.

ECTENOCERAS COMPRESSUM Ulrich, Foerste, & Miller

Pl. 51, fig. 9–14

Ectenoceras compressum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. Am., Special Paper 49, p. 119, pl. 57, fig. 1,2.

This species is represented in the Chepultepec collection by 27 specimens. Most of these are very fragmental but exhibit clearly the distinguishing characters of the species. However two are somewhat more complete but even these leave much to be desired. The larger of the two is 13 mm. long, 14.2 mm. high, and 12.3 mm. wide. It is very slightly expanded orad. The second specimen is about 22 mm. long. Near the mid-length it is 10 mm. high and 8 mm. wide, and in this specimen the expansion is slightly more rapid in the adoral portion. All specimens are compressed to a narrowly oval cross-section.

The camerae in all the specimens are very short, averaging less than 1 mm. The septa are rather strongly curved and the sutures form asymmetrical lateral lobes with low dorsal and high ventral saddles. The siphuncle is slightly compressed. It is ventral in position and at the adoral end of the largest specimen is 3 mm. high.

Remarks.—These specimens are slightly distorted so that the siphuncle is slightly off-center. In some the displacement is to the right and in others to the left, but it is obvious that the displacement is not a natural growth feature.

Occurrence.—Locality 1. The holotype of this species is from the Gasconade of Franklin County, Mo.

Repository.—Univ. Mo. 12717a–f, 12718.

ECTENOCERAS EXILE Ulrich Foerste, & Miller

Pl. 51, fig. 15,16

Ectenoceras exile ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. Am., Special Paper 49, p. 120, pl. 57, fig. 24,25.

Five specimens from the Chepultepec are being referred to this species. All are septate throughout and represent only phragmocones. They are all curved endogastrically and the curvature is more pronounced in the adapical end. They expand orad at a moderate rate. These specimens have been slightly distorted in cross-section but it seems that they were compressed laterally and were oval with the dorsum being slightly more narrowly rounded than the venter. The largest of the four is 20 mm. long, and at the adoral end it is 6 mm. high and 4.5 mm. wide.

The camerae are very short, about three

in a length of 1 mm. The sutures slope slightly apicad from the dorsum to the venter and are essentially straight. The siphuncle is compressed laterally but appears to have been distorted. It is small, ventral in position, but not in contact with the shell wall.

Remarks.—These specimens are different from *E. compressum* in being smaller and less strongly compressed. They also have a smaller siphuncle.

Occurrence.—Locality 1. The only other known specimens of this species are from the Gasconade of Miller County, Missouri.

Repository.—Univ. Mo. 12719, 12720.

ECTENOCERAS LONGUM Ulrich, Foerste, & Miller
Pl. 51, fig. 17,18

Ectenoceras longum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. Am., Special Paper 49, p. 122–123, pl. 57, fig. 5,6.

This species appears to be represented in the Chepultepec collection by a single specimen which represents a part of a phragmocone. It is 20 mm. long and near the mid-length it is 6 mm. wide and 7.3 mm. high. The septa are slightly curved laterally but more strongly so dorso-ventrally. They slope apicad from the venter. The sutures form broad shallow rounded lateral lobes which center close to the dorsum. They form low dorsal, and higher ventral, saddles.

The siphuncle is somewhat displaced because of distortion but it appears to have been in contact with the ventral wall of the shell. It is about 1.5 mm. in diameter.

Remarks.—It is difficult to compare this specimen with the holotype of the species, because they represent different parts of the shell. However, they seem to supplement each other and are similar in size, cross-section, and in slender proportions.

Occurrence.—Locality 1. The holotype of this species is from the Tanyard of San Saba County, Texas.

Repository.—Univ. Mo. 12721.

Genus ALBERTOCERAS Ulrich & Foerste, 1936

ALBERTOCERAS STAUFFERI Ulrich, Foerste, Miller, & Unklesbay
Pl. 51, fig. 19–21

Albertoceras staufferi ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944, Geol. Soc. Am., Special Paper 58, p. 62–63, pl. 23, fig. 1–7.

Four specimens from the Chepultepec are being referred to this species. All are essentially straight longicones which expand orad rather gradually. All are elliptical in cross-section being compressed laterally, and all are septate throughout. The largest specimen is 26 mm. long. Near its mid-length it is 6.2 mm. high and 3.7 mm. wide. The next largest one is 18 mm. long, and the next is about 14 mm. The fourth specimen is somewhat more compressed but is otherwise like the others.

In all these specimens the camerae are very short; less than 1 mm. each. The septa are directly transverse and the sutures form slight lateral lobes and low dorsal and ventral saddles. In the smallest specimen the sutures are slightly distorted because of crushing.

The siphuncles in these specimens are near the ventral wall, but they are not well preserved and their structure is not clearly exposed.

Remarks.—The septa in these three specimens are more closely spaced than in most congeneric forms but otherwise they are closely similar to previously described forms.

Occurrence.—Locality 1. The type specimens of this species are from the Tanyard of San Saba County, Texas.

Repository.—Univ. Mo. 12722a–c, 12723.

Genus CLELANDOCERAS Ulrich, Foerste, Miller, & Unklesbay, 1944

CLELANDOCERAS ELONGATUM Ulrich, Foerste, Miller & Unklesbay
Pl. 51, fig. 22,23

Clelandoceras elongatum ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944, Geol. Soc. Am., Special Paper 58, p. 134–135, pl. 3, fig. 8–10.

The collection being studied contains eight specimens referable to this species. All are rather strongly curved with the siphuncle being on the concave side. They expand orad rather rapidly. They are compressed laterally and are oval to elliptical in cross-section.

The largest of these specimens is about 17 mm. long. The height increases from 3.3 mm. at the adapical end to 8 mm. at the adoral end. In the same distance the width increases from 2 mm. to 4 mm. The other specimens have the same relative proportions.

All these specimens represent phragmo-

cones and are septate throughout. The septa are very closely spaced, there being three in a length of 1 mm. The sutures form very shallow lateral lobes and low ventral and dorsal saddles. The dorsal saddle is slightly higher than the ventral. The siphuncle is small, being less than 1 mm. in the largest specimen. Its structure is not well preserved, but it seems to have had nearly straight septal necks and connecting rings.

Remarks.—These specimens seem very close to the holotype in all respects.

Occurrence.—Locality 1. The type of this species are from the Smithville formation in Lawrence County, Arkansas.

Repository.—Univ. Mo. 12724, 12725.

Genus ANGULOCERAS, n. gen.

Type species: *Anguloceras ovatum*, n. sp.

Conch moderate in size, slender, nearly straight, slightly expanded orad. Subcircular to elliptical in cross-section. Camerae very short. Septa slope steeply apicad from venter to dorsum. Sutures straight laterally, but slope of septa causes them to form deep dorsal lobes and high ventral saddles. Siphuncle moderate in size, ventral and marginal in position and composed of cylindrical segments.

The most obvious characteristic of this genus is the steep slope of the septa, and this feature serves to differentiate it from other forms.

ANGULOCERAS OVATUM, n. sp.
Pl. 51, fig. 24–26

Four silicified internal molds of phragmocones form the basis for this species. The largest and best is designated as the holotype. It is essentially straight, moderately tapered, and is oval in cross-section. The dorsum is more narrowly rounded than the venter. The specimen is 20 mm. long, and at the adoral end is 9.5 mm. wide and 11.6 mm. high.

The camerae are very short, averaging about 0.3 mm. each. The septa are exceedingly shallow and slope apicad from the venter to the dorsum making an angle of about 43 degrees with the ventral side of the shell. The sutures are straight across the lateral zones but form high ventral saddles and deep dorsal lobes. The siphuncle is moderate in size, being about 2 mm. in diameter and very slightly depressed in cross-section. It is ventral and marginal in position.

Remarks.—The paratypes of this species are all fragmentary silicified internal molds of phragmocones. They resemble the holotype very closely. This species can be differentiated from other congeneric forms by its oval cross-section.

Occurrence.—Locality 1.

Types.—Univ. Mo. holotype 12726; Paratype 12727.

ANGULOCERAS DEPRESSUM, n. sp.
Pl. 51, fig. 27,28

This species is based on one specimen which is a silicified internal mold of a portion of a phragmocone. It is straight, slightly expanded orad, and depressed to elliptical cross-section. It is 17 mm. long and at the adoral end is 9.5 mm. wide and 6.3 mm. high.

The septa are convex apicad and slope steeply apicad from venter to dorsum, making an angle of about 50 degrees with the long axis of the conch. The siphuncle is moderate in size and depressed dorso-ventrally to an elliptical cross-section. It is about 2.2 mm. wide at the adoral end, and is ventral and marginal in position.

Remarks.—This species has the same steeply sloping septa as other congeneric forms but can be separated from them by the depressed elliptical cross-section.

Occurrence.—Locality 1.

Holotype.—Univ. Mo. 12728.

ANGULOCERAS ROTUNDUM, n. sp.
Pl. 52. fig. 13,14

Only one specimen is used as the basis for this species and it is therefore the holotype. It is a silicified internal mold of a phragmocone about 25.6 mm. long. It is slightly curved endogastrically with the curvature being more pronounced in the adapical portion. It expands gradually orad. The cross-section is circular with a very faint flattening on the venter. At the adoral end this specimen is 9 mm. in diameter.

The camerae are very short, averaging about 3 to a length of 1 mm. The septa are faintly concave and slope steeply apicad from the venter to the dorsum making an angle of about 55 degrees with the venter. This angle is slightly steeper at the adoral end. The siphuncle is moderate in size and slightly de-

pressed dorso-ventrally. At the adoral end it is 2.1 mm. wide. It appears to have been in contact with the ventral wall of the conch.

Remarks.—This species can be separated from *A. ovatum* by the lesser steepness of the septa and by the more nearly circular cross-section. One other specimen is being referred to this species with some question. It has steeply sloping septa and appears to have been distorted from an original circular cross-section.

Occurrence.—Locality 1.

Holotype.—Univ. Mo. 12729.

Family CYCLOSTOMICERATIDAE Foerste
Genus WOOSTEROCERAS Ulrich, Foerste, Miller, & Unklesbay, 1944

WOOSTEROCERAS CHEPULTEPECENSE, n. sp.
Pl. 52, fig. 1–4

This species is being based on seven closely similar specimens all of which are silicified internal molds representing only phragmacones. They are all slightly distorted, but it seems certain that before the distortion took place they were curved endogastrically and were circular or nearly so in cross-section. They are distinctly but not greatly expanded orad.

The largest specimen is about 20 mm. long. At the adapical end it was about 5 mm. in diameter before distortion and at the adoral end about 8 mm. The others are of approximately the same magnitude and proportion but represent less complete specimens.

The septa are very closely spaced; there being about seven in a length of 2 mm., and they are very shallow. The siphuncle is small, circular in cross-section, and very close to the ventral wall. At the adoral end of the large specimen it is slightly over 1 mm. in diameter.

The large specimen bears traces of growth lines which seem to indicate that the aperture was slightly oblique and sloped apicad toward the dorsum.

Remarks.—Despite the distortion of these specimens their generic characteristics are obvious. They are very similar to previously described congeneric forms but are more rapidly expanded than *W. trempeleauense*, and the septa are more closely spaced than in *W. cherokeense*.

Occurrence.—Locality 1.

Repository.—Univ. Mo. syntypes 12730.

Family BALTOCERATIDAE Kobayashi
Genus PACHENDOCERAS Ulrich & Foerste, 1936

PACHENDOCERAS CONFERTUM Ulrich, Miller, & Unklesbay
Pl. 52, fig. 7,8

Pachendoceras confertum ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944 Geol. Soc. Am., Special Paper 58, p. 121–122, pl. 63, fig. 6–9.

Three specimens from the Chepultepec collection are referred to this species. The best one is 17 mm. long, 13 mm. wide, and 9.5 mm. high. It is septate throughout and appears to have been straight. It is subcircular in cross-section, being somewhat depressed dorso-ventrally.

The septa are shallow and very closely spaced, and the camerae are about 0.5 mm. in length. They slope apicad from the venter, forming slight ventral saddles in the sutures, but otherwise the sutures are essentially straight. The siphuncle is large, broadly elliptical, and depressed. It is about 6 mm. wide and 3 mm. high, and was apparently in contact with the ventral wall.

Remarks.—The other two specimens are similar in most respects but are slightly smaller and less well preserved. This species is rather conspicuous because of the large size of the siphuncle and the close spacing of the septa.

Occurrence.—Locality 1. This species is also known from the Gasconade in Crawford County, Missouri.

Repository.—Univ. Mo. 12732, 12733.

PACHENDOCERAS BREVICAMERATUM, n. sp.
Pl. 52, fig. 5,6

The holotype of this species is a portion of a somewhat distorted phragmocone, about 37 mm. long. The cross-section in the present specimen is elliptical but it is obvious that the original shape was subcircular. The distortion is made clear by the fact that the siphuncle is in an asymmetrical position, and the septa slope at an unnatural angle. It appears that if the specimen could be squeezed back to a subcircular cross-section the septa and siphuncle would resume normal positions. The present height of the specimen is 15 mm. and the width is 9 mm. If restored to original shape the shell would be about 12 mm. in diameter.

The camerae are unusually short, averag-

ing less than 0.5 mm. each. The sutures were apparently straight and essentially transverse. The septa were moderately convex apicad.

Remarks.—Three other fragmentary specimens of this species are available and they are also distorted. One of them has the siphuncle asymmetrical on the opposite side than in the holotype.

Occurrence.—Locality 1.

Repository.—Univ. Mo. holotype 12734; others 12735.

PACHENDOCERAS PARVUM, n. sp.
Pl. 52, fig. 9–12

Six specimens are being used as a basis for this species. They are somewhat smaller than the type species of the genus but they are similar in most other respects. They are all septate throughout. They are longiconic, slender, and nearly straight. The cross-section is nearly round but slightly depressed as the venter is slightly flattened. The two larger specimens are nearly the same size. The better of the two is chosen as a holotype. It is 28 mm. long, and at the adoral end it is 8 mm. high and 11 mm. wide.

The septa are very closely spaced, being about 0.5 mm. apart, and the sutures are essentially straight and directly transverse. The siphuncle is ventral in position and in contact with the shell wall. It is elliptical in cross-section being depressed. At the adoral end of the holotype it is 2 mm. wide.

Remarks.—These specimens do not have a well-developed spiculum as do most forms in this genus. However, the holotype has a siphuncular filling resembling a rudimentary spiculum.

Occurrence.—Locality 1.

Syntypes.—Univ. Mo. 12736, six syntypes.

Order BASSLEROCERATIDA Flower
Family BASSLEROCERATIDAE Ulrich, Foerste, Miller, & Unklesbay
Genus BASSLEROCERAS Ulrich & Foerste, 1936
BASSLEROCERAS cf. B. BRIDGEI Ulrich, Foerste, Miller, & Unklesbay
Pl. 52, fig. 15,16

One specimen in this collection is a small portion of a phragmocone about 17 mm. long. It is broadly elliptical in cross-section, being compressed laterally. The camerae are very short, averaging about 0.5 mm. The septa are oblique, sloping strongly apicad from the venter to the dorsum. The sutures form high ventral saddles, asymmetrical lateral lobes, and low rounded dorsal saddles. The siphuncle is circular in section and is moderately large. Near the mid-length of the specimen where the height is 9.5 mm. and the width 7.4 mm. the siphuncle is about 2.2 mm. in diameter. It is ventral in position but not in contact with the ventral wall.

Remarks.—This specimen does not seem to be conspecific with any described species and is not adequate to form the basis for a new species. It seems closer to *B. bridgei* than to any other species.

Occurrence.—Locality 1.

Repository.—Univ. Mo. 12737.

CHEPULOCERAS, n. gen.

Type species: *Chepuloceras inelegans*, n. sp.

Conch small, longiconic, curved exogastrically, depressed ventrally. Camerae short. Sutures form shallow lateral lobes and low ventral and high dorsal saddles. Siphuncle moderate in size, ventral and nearly marginal. Septal necks not definitely known but appear to be holochoanitic. Living chamber not known.

Only one species is presently being referred to this genus but it is distinct from previously described forms.

This genus appears to belong with the Bassleroceratidae. It differs from most of the genera in this family in being depressed ventrally and in having sutures with low ventral and high dorsal saddles.

CHEPULOCERAS INELEGANS, n. sp.
Pl. 52, fig. 17,18

The holotype and only known specimen of this species is a silicified internal mold of a phragmocone about 35 mm. long. It is curved exogastrically with the ventral side being more strongly curved than the dorsal. It is depressed ventrally, more strongly so in the more advanced parts of the shell, so that the cross-section is sub-rounded. The specimen tapers gradually from a width of 3.8 mm. at the adapical end to 10.1 mm. at the

adoral end. The height at the adoral end is 7.5 mm.

The septa are very closely spaced, being less than 0.5 mm. apart. They slope steeply orad from the venter to the dorsum so that the sutures form low ventral and high arched dorsal saddles. The siphuncle is moderate in size. At the adoral end of the specimen the siphuncle is depressed to an elliptical cross-section, and is about 2 mm. wide. It is close to, but not in contact with, the ventral wall.

Remarks.—This species is different from previously described forms in having a ventrally depressed cross-section combined with steeply sloping septa, and high arched dorsal saddles in the sutures. The holotype is slightly distorted in the adapical end.

Occurrence.—Locality 1.

Holotype.—Univ. Mo. 12738.

REFERENCES

BASSLER, R. S., 1919, The Cambrian and Ordovician deposits of Maryland: Maryland Geol. Survey, 424 p.

BUTTS, CHARLES, 1933, Geologic Map of the Appalachian Valley of Virginia with explanatory text: Virginia Geol. Survey, Bull. 42, 56 p.

——, 1940, Geology of the Appalachian Valley in Virginia: Virginia Geol. Survey, Bull. 52, pt. I, 568 p.

EDMUNDSON, R. S., 1945, Industrial limestones and dolomites in Virginia: Northern and central parts of Shenandoah Valley: Virginia Geol. Survey, Bull. 65, 195 p.

MILLER, R. L., & FULLER, J. O., 1954, Geology and oil resources of the Rose Hill district, Virginia: Virginia Geol. Survey, Bull. 71, 383 p.

ODER, C. R. L., 1934, Preliminary subdivision of the Knox dolomite in east Tennessee: Jour. Geology, vol. 42, p. 469–497.

RODGERS, JOHN, 1953, Geologic map of east Tennessee, with explanatory text: Tennessee Div. Geology, Bull. 58, pt. II, 168 p.

STOSE, G. W., 1908, The Cambro-Ordovician limestones of the Appalachian Valley in southern Pennsylvania: Jour. Geology, vol. 16, p. 698–714.

TWENHOFEL, W. H., et al., 1954, Correlation of the Ordovician formations of North America; Geol. Soc. Am., Bull., vol. 65, p. 247–298.

ULRICH, E. O., 1911, Revision of the Paleozoic systems: Geol. Soc. Am., Bull., vol. 22, p. 281–680.

——, FOERSTE, A. F., & MILLER, A. K., 1943, Ozarkian and Canadian cephalopods. Part II, Brevicones: Geol. Soc. Am. Special Paper 49, 240 p., 70 pl., 15 fig.

——, ——, ——, & UNKLESBAY, A. G., 1944, Ozarkian and Canadian cephalopods. Part III, Longicones and summary: Geol. Soc. Am., Special Paper 58, 226 p., 68 pl., 9 fig.

UNKLESBAY, A. G., 1954, Nautiloids from the Tanyard formation of central Texas: Jour. Paleont., vol. 28, p. 637–656, pl. 68–71.

WILSON, J. L., 1952, Upper Cambrian stratigraphy in the central Appalachians: Geol. Soc. Am. Bull., vol. 63, p. 275–322.

WOODWARD, H. P., 1951, Ordovician system of West Virginia: West Virginia Geol. Survey, vol. 21, 627 p.

MANUSCRIPT RECEIVED SEPTEMBER 19, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 492–503, PL. 53–56, 7 TEXT-FIG., MAY 1956

UPPER CRETACEOUS AND EARLY TERTIARY NAUTILOIDS FROM WESTERN AUSTRALIA

BRIAN F. GLENISTER, A. K. MILLER, AND W. M. FURNISH
State University of Iowa, Iowa City

ABSTRACT—Representative collections from the North West Cape area in the northern part of the Carnarvon Basin contain one species of Upper Cretaceous nautiloids, one of Paleocene, and three of Eocene. These are described as *Cimomia tenuicosta*, n. sp., *Teichertia prora*, n. gen., n. sp.; *Aturoidea brunnschweileri*, n. sp.; *A.* sp.; and *Aturia* cf. *A. clarkei* Teichert.

INTRODUCTION

MESOZOIC and Tertiary nautiloids have long been known from Western Australia. However, until recently the collections have been small and the number of species few. The past decade has witnessed an impressive increase in our knowledge of the stratigraphy of Western Australia. This has resulted largely from extensive researches by Curt Teichert, the Commonwealth of Australia Bureau of Mineral Resources, and several oil companies. The present report deals with the large and significant collections of Upper Cretaceous and early Tertiary nautiloids assembled during the active stratigraphic studies conducted in the Carnarvon (Northwest) Basin over the past score of years.

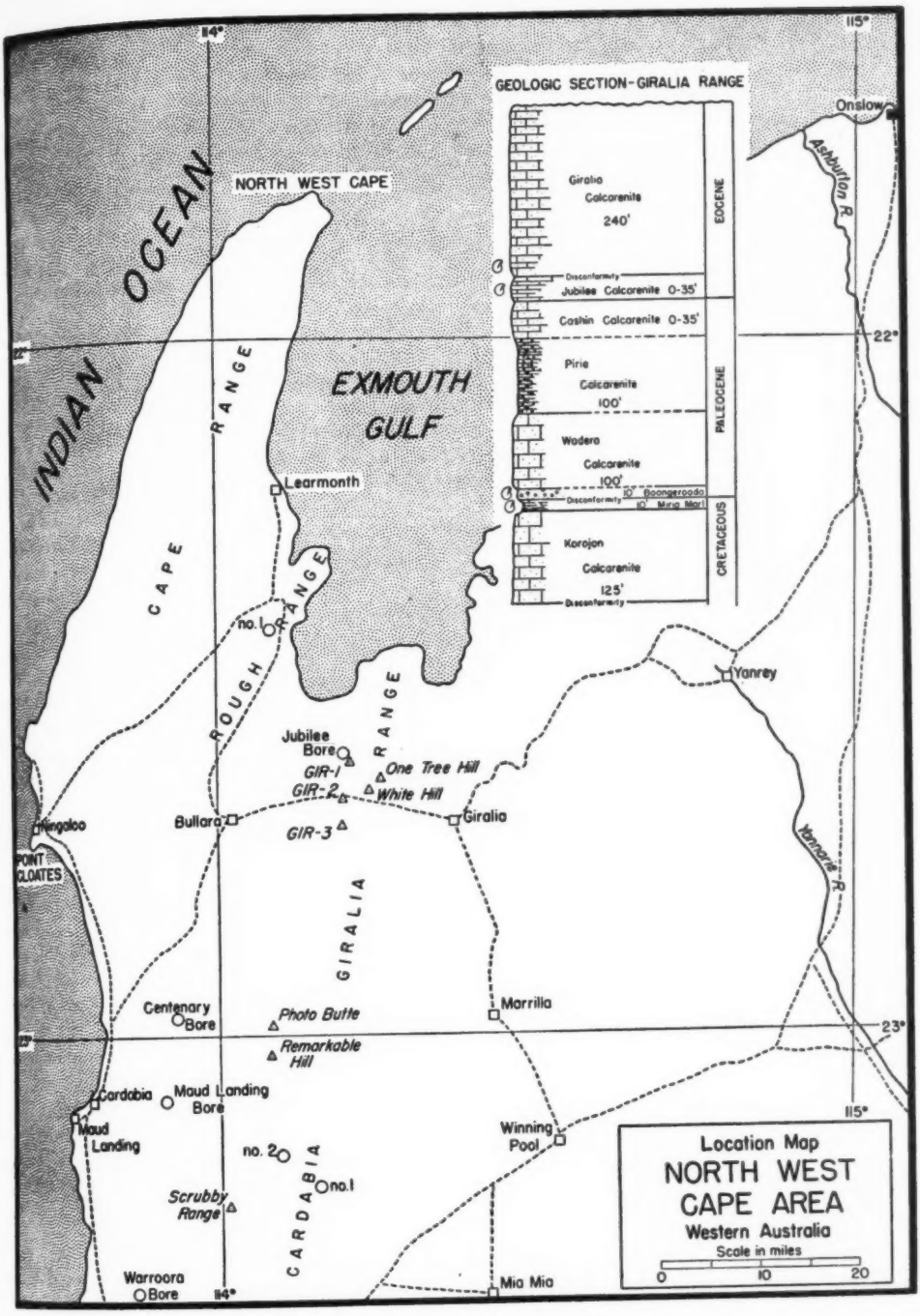
Most of the rock units used in the present study have only recently been named and defined. The latest comprehensive account of the Carnarvon Basin stratigraphy is that by Condon (1954). The relevant part of the stratigraphic sequence is portrayed in Text-figure 1 of the present report; readers are referred to Condon's work for more detailed information.

The present study was facilitated by many individuals. The collections were made available by the Director of the Commonwealth of Australia Bureau of Mineral Resources. Officers of that Bureau who provided stratigraphic data include Irene Crespin, M. A. Condon, R. O. Brunnschweiler (now of Geosurveys of Australia, Ltd.), G. A. Thomas, and S. Henderson. Curt Teichert read the manuscript. Acknowledgment is also due to Frederick D. Leach, who retouched the accompanying photographs. The work was made financially possible by the Graduate College of the State University of Iowa. One of us (B. F. G.) undertook the study during the period of tenure of a Fulbright Scholarship.

HISTORICAL SUMMARY

The credit for the earliest report of either Cretaceous or Tertiary nautiloids from Western Australia goes to Jutson & Simpson (1916, p. 24), who recorded *Aturia australis* (McCoy) from the "Plantagenet Series" near Albany, southwestern Australia. In the following year, these same authors gave further details concerning the occurrence of the species near Albany; and they stated that it had also been discovered at Cape Riche, some 50 miles to the east, and at Bremer Bay, a further 50 miles east. Newton (1919) next recorded *Aturia* from the same general locality; he referred the specimens to *A. aturi* (Basterot), for he regarded *A. australis* as a synonym of that European species. In their account of the paleontology of the "Plantagenet Series," Chapman & Crespin (1934) again listed *A. australis* from near Albany, and they supported Jutson & Simpson's reference of this group to the Miocene.

The next report of *Aturia* from Western Australia was by Condit, Raggat, & Rudd (1936, p. 1059). They recorded a single specimen from near Merlinleigh Homestead, some 750 miles north of the previous localities, and 90 miles inland from the nearest outcrops of Tertiary sediments known at that time. The description of the specimen by Miller & Crespin followed in 1939. These authors noted that it is not closely similar to the type material of *A. australis*, and in view of the uncertainty in regard to its age, they referred it to a European species, *A. ziczac*



TEXT-FIG. 1—Partly after Condon.

(Sowerby). Further collections of *Aturia* from near Merlinleigh Homestead prompted Teichert (1944) to undertake a comprehensive study of the Australian occurrences of this genus. It was shown that all the known Western Australian specimens were conspecific, and the name *A. clarkei* was proposed for them. Chapman & Crespin (1934) had determined the age of the Plantagenet group as early Miocene, and in the absence of contradictory evidence, Teichert assumed a Miocene age for all the beds containing *A. clarkei*.

The Western Australian Cretaceous and Tertiary nautiloids have been briefly reviewed by Teichert (*in* Teichert & Glenister, 1952). He reported a new species of both *Cymatoceras* and *Cimomia* from beds of late Campanian to early Maestrichtian age in the Carnarvon Basin, and a species of *Aturoidea* from strata of late Maestrichtian age in the same general area. *Aturoidea*, *Deltoidonautilus*, and *Hercoglossa* were reported from sandstones and sandy limestones of Middle to Upper Eocene age.

STRATIGRAPHY

The Carnarvon Basin is a large tectonic feature which can be traced southward for some 400 miles, from the vicinity of Onslow to the Murchison River. It is elongate in a north-south direction. At its broadest part, it extends inland from the Indian Ocean for about 130 miles. The axis probably lies some 30 miles to the east of Cape Cuvier.

The Basin is known to contain a more or less conformable sequence of sandstones, graywackes, shales, and limestones, which range in age from Middle Devonian to late Permian. These sediments have been measured near the eastern margin of the Basin, where they attain a cumulative thickness of some 20,000 feet. Unconformably overlying the Paleozoic sediments is a sequence of siltstones, radiolarites, and limestones, which range in age from Middle Jurassic to Recent. Several uncomformities and numerous disconformities are known within this latter succession. A maximum thickness of 3,600 feet has been compiled for these beds.

Nautiloids are known from three formations in the Cardabia group (Miria marl, Boongerooda greensand, and Jubilee calcarenite), from the overlying Giralia calcarenite, and from the Merlinleigh sandstone. The cephalopods occur in direct association with rich assemblages of both macro- and microfossils.

The Cardabia group is characterized by the development of glauconitic calcarenites, but it contains smaller thicknesses of calcilutites, marls, and greensands. Condon (1954, p. 114–117) has subdivided the Cardabia group, from the base upward, into the Korojon calcarenite, the Miria marl, the Boongerooda greensand, and the Wadera, Pirie, Cashin, and Jubilee calcarenites. Brunnschweiler (personal communication) has determined that the few ammonoids known from the Korojon calcarenite are of late Santonian to early Campanian age. The overlying Miria marl contains a large fauna, including a rich and highly varied assemblage of late Campanian or early Maestrichtian ammonoids. *Cimomia tenuicosta*, n. sp., is restricted to this formation. The overlying Boongerooda greensand contains a foraminiferal fauna, and this formation is the source of the specimens described herein as *Aturoidea* sp. It may possibly be late Maestrichtian, but it is generally considered as earliest Paleocene. The remaining formations of the Cardabia group consist of a conformable sequence of calcarenites, ranging in age from Paleocene to Middle Eocene. Condon (1954) places all four formations in the Paleocene, but Brunnschweiler (personal communication) considers the youngest, Jubilee calcarenite, to be Lutetian (Middle Eocene). *Teichertia prora* and *Aturoidea brunnschweileri*, n. spp., are represented by several specimens from near the top of the Jubilee calcarenite.

The Giralia calcarenite overlies the Ju-

EXPLANATION OF PLATE 53

FIG. *1–9—Cimomia tenuicosta*, n. sp. Four specimens from the Upper Cretaceous Miria marl of the Giralia-Cardabia Range, Western Australia. *1–3*, holotype (1714), ×1½; *4*, paratype (1715), ×1¼; *5–7*, paratype (1717), ×1½; *8,9*, paratype (1716), ×1½. (p. 495)

1

5

8

4

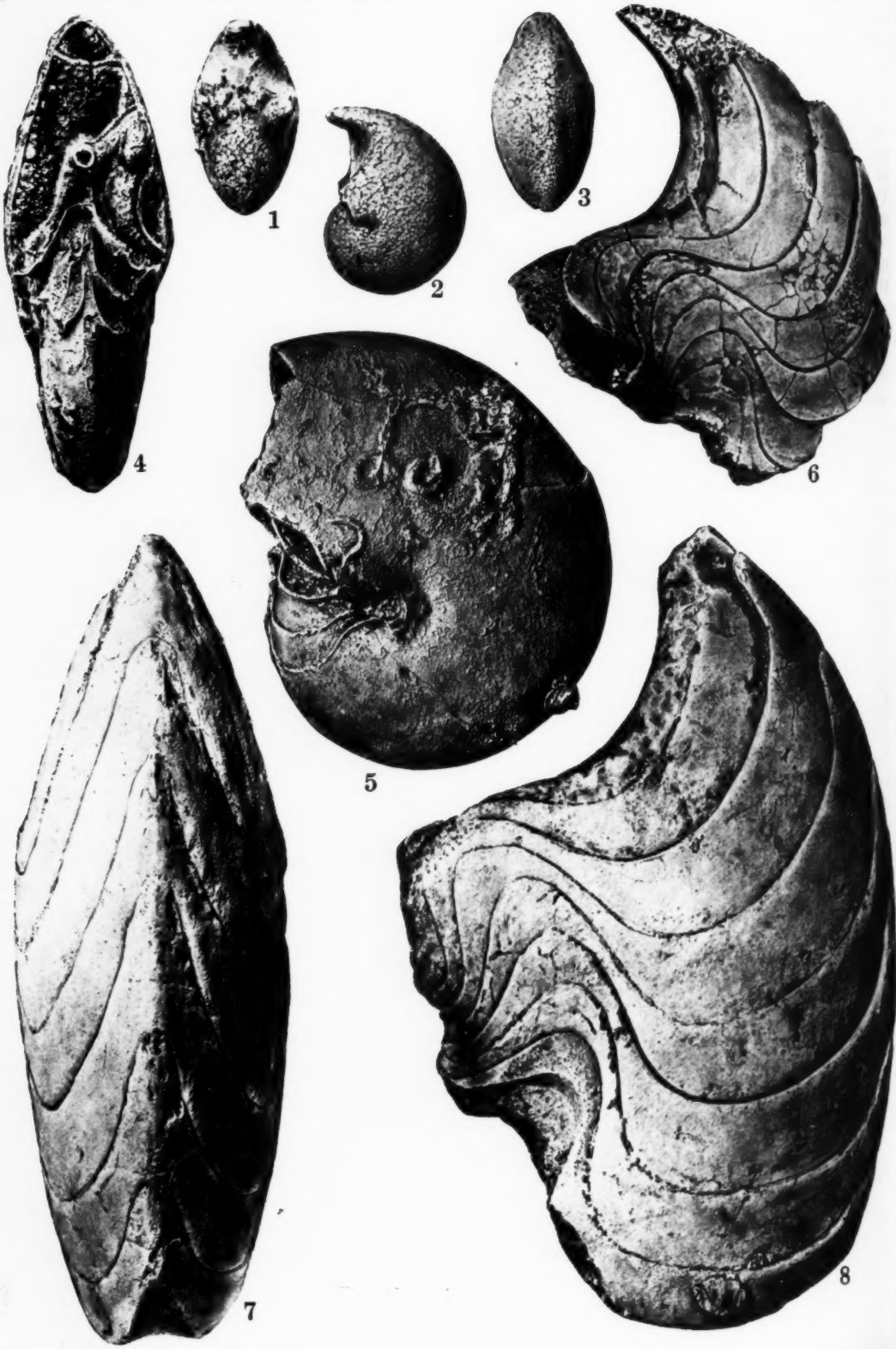
6

9

2

7

3


1
2
3
4
5
6
7
8

bilee calcarenite. From it Edgell (1952, unpublished report) has identified *Alveolina* cf. *A. timorensis*, *Asterocyclina* spp., *Assilina orientalis*, *Discocyclina* spp., *Nummulites* aff. *N. irregularis*, *Globorotalia spinulosa*, and *Victoriella plecte*. Condon (1954, p. 118) believed that this fauna places the Giralia calcarenite in the "a" to "b" stages (van der Vlerk, 1948) of the East Indies succession, which van Bemmelen (1949) stated to be Middle to Upper Eocene. Brunnschweiler has determined that both this formation and the underlying Jubilee calcarenite are Lutetian (Middle Eocene). Most of the known representatives of *Teichertia prora* and *Aturoidea brunnschweileri* are from the Giralia calcarenite. They occur in association with the specimens described herein as *Aturia* cf. *A. clarkei* Teichert.

The two remaining Tertiary rock units in Western Australia from which nautiloids have been recorded are the Plantagenet group and the Merlinleigh sandstone. Each contains *A. clarkei*. The Plantagenet group is widely developed in the Albany area, on the south coast of Western Australia. This sequence has long been considered to be Miocene, and Chapman & Crespin (1934) placed it in the early Miocene. The Merlinleigh sandstone is a coarse- to medium-grained quartzose sandstone, which is developed in the Kennedy Range near Merlinleigh Station. It lies, with angular unconformity, on the Korojon calcarenite or older beds. The first collections of fossils from the Merlinleigh sandstone were scanty. However, they contained *Aturia clarkei*, and therefore Teichert (1944) assumed a Miocene age for the formation. Recent detailed field work has revealed the presence of a large fauna of pelecypods, gastropods, and echinoids, which Brunnschweiler (personal communication) believes to be Lutetian. A Lutetian age is also currently favored for the Plantagenet group. Our work is in accord with these age revisions, for we are describing *Aturia* cf. *A. clarkei* from the Lutetian Giralia calcarenite.

SYSTEMATIC PALEONTOLOGY

Genus CIMOMIA Conrad, 1866

Type species: *Nautilus Burtini* Galeotti, 1837

CIMOMIA TENUICOSTA, n. sp.

Pl. 53, fig. 1–9

Cymatoceras n. sp. and *Cimomia* n. sp. TEICHERT, 1952, Jour. Paleont., vol. 26, p. 737.

A single species of nautiloids is known from the uppermost Cretaceous of the Giralia-Cardabia Range. It occurs abundantly, and 40 specimens are available for study. All of these are septate throughout, and several of the larger have a uniform maximum overall measurement of some 75 mm., suggesting that this was the size of the mature phragmocone. Near the adoral end of one of these (Pl. 53, fig. 4), which appears to be free from distortion, the conch is about 45 mm. high and 50 mm. wide.

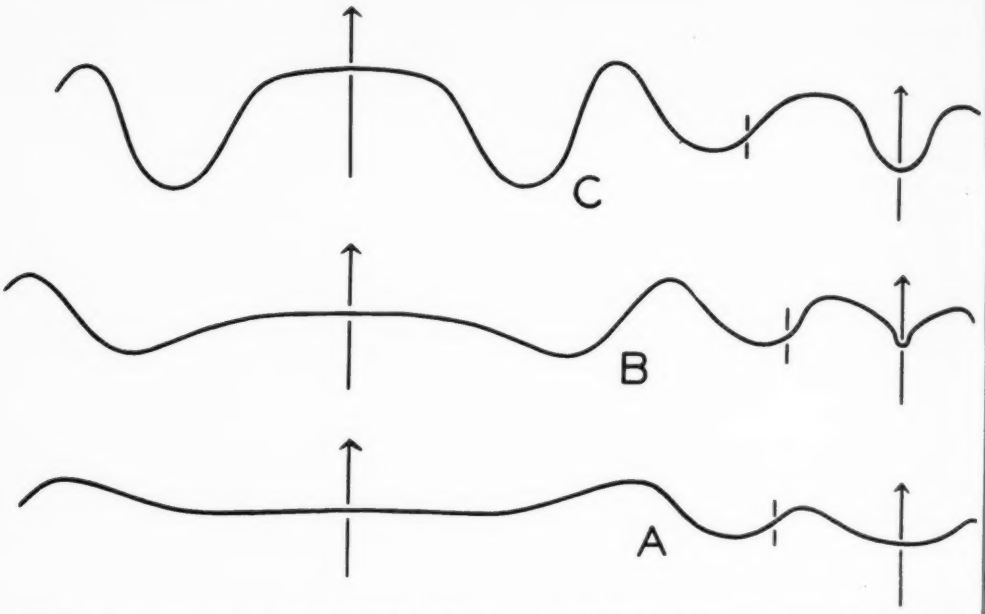
The umbilicus is small and inconspicuous. It was filled with a callus. The test is moderate in thickness. Its surface bears sinuous transverse costae which are parallel to the growth lines and form a rounded ventral sinus and broad rounded lateral salients. No trace of these is retained on the internal mold.

Each suture (Text-fig. 2B) forms a low broad ventral saddle and on either side of it a rounded lateral lobe, a prominent narrowly rounded saddle near the umbilicus, a shallow lobe on the umbilical wall, and a rounded internal lateral saddle which extends to the broad dorsal lobe. In the center of the dorsal lobe there is a small U-shaped annular lobe.

The siphuncle is small and is located fairly close to the venter. Where the conch of the holotype (Pl. 53, fig. 1–3) is about 30 mm. high, the siphuncle is about 1½ mm. in diameter, and its center is about 4 mm. from the venter.

EXPLANATION OF PLATE 54

FIG. *1–8*—*Teichertia prora*, n. sp. Four specimens from the Middle Eocene Giralia calcarenite of the Giralia Range, Western Australia. *1–3*, paratype (1701), ×1¾; *4,5*, paratype (1702), ×1½; *6*, holotype (1700), ×9/10; *7,8*, paratype (1703), slightly more than ×½. (p. 497)



TEXT-FIG. 2—Sutures of **(A)** a typical *Cimomia*, *C. landanensis* (Vincent), from the Paleocene of Angola, ×½; **(B)** *C. tenuicosta*, n. sp., from the Maestrichtian Miria marl of the Cardabia Range in Western Australia, ×1; and **(C)** an advanced *Hercoglossa*, *H. orbiculata* (Toumey), the type species of the genus, from the Paleocene of Alabama, ×¼.

Remarks.—The smallest figured specimen (Pl. 53, fig. 5–7) is not typical of the species. This individual, but not others of comparable size, has camerae which are singularly variable in length. During early adolescence, the septa were closely spaced, with a resultant modification in the shape of the suture. In addition, the adapical portion of the outer volution of this specimen retains faint traces of reticulate sculpture.

As shown by Plate 53, figure 3, the position of the siphuncle varies during ontogenetic development. Also, its apparent position on Plate 53, figure 8, is misleading, because of foreshortening.

The surface markings of this species are somewhat reminiscent of those on *Cymatoceras* and *Paracymatoceras*. However, in those genera the transverse ribs are less numerous and more prominent, and they are reflected on the inner surface of the test.

The sutures of the form under consideration are more or less intermediate between those of typical *Cimomia* and typical *Hercoglossa* (Text-fig. 2). However, they show a closer resemblance to those of the former.

Occurrence.—Miria marl (Campanian-Maestrichtian) at three localities in the Giralia-Cardabia Range of Western Australia. The holotype and two of the figured paratypes (1715, 1716) are from two gullies near One Tree Hill (between it and White Hill). The other figured paratype (1717) is from Remarkable Hill. The remaining unfigured paratypes are from these two localities as well as Photo Butte Hill, which is a few miles north of Remarkable Hill.

Repository.—Commonwealth of Australia Bureau of Mineral Resources, Canberra. Holotype, catalogue no. 1714; figured paratypes, 1715–1717; unfigured paratypes, 1762.

Genus TEICHERTIA, n. gen.

Type species: *Teichertia prora*, n. sp.

This genus is established to accommodate a single new species, which is related to typical *Deltoidonautilus* but differs materially in the shape of the cross section and the form of the suture. In *Teichertia* the venter is acutely angular rather than narrowly rounded, and each suture forms a total of seven lobes (rather than five). The lateral and ventral saddles are relatively promi-

nent, the dorsal lobe is narrow, and the umbilical lobe is divided. The genus is believed to have evolved from *Deltoidonautilus*, some representatives of which have comparable proportions and likewise attain maximum overall dimensions of as much as 400 mm. The single known species of *Teichertia* is from the Middle Eocene of Western Australia, whereas *Deltoidonautilus*, which is widespread geographically, has been found to range from the late Cretaceous (upper Maestrichtian) to the Middle Eocene. The generic name is given in honor of Curt Teichert.

TEICHERTIA PRORA n. sp.
Pl. 54, fig. 1–8

Deltoidonautilus sp. and *Hercoglossa* sp. TEICHERT 1952, Jour. Paleont., vol. 26, p. 737–738; CONDON, 1954, Australia Bur. Min. Res., Rept. 15, p. 117, 118.

We are basing this species on 15 specimens. These are fragmentary but collectively portray most of the more significant characters. They represent various growth stages of the phragmocone, ranging in maximum overall diameter from about 15 mm. to 300 mm. (estimated).

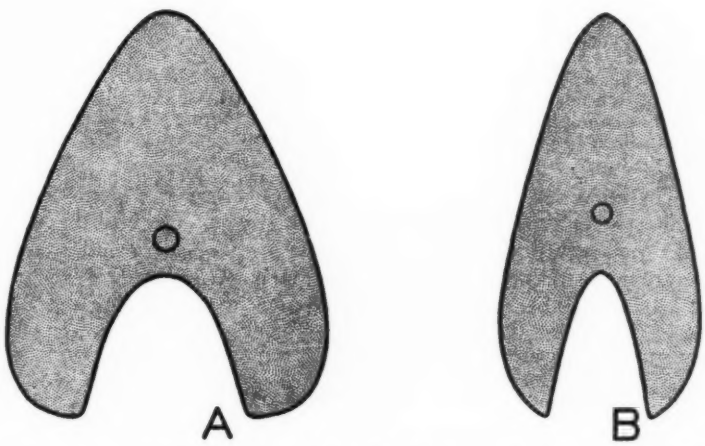
During early ontogenetic development, the conch is thickly lenticular, being broadly rounded laterally, narrowly rounded across the venter, and moderately impressed dorsally. Larger specimens develop relatively narrow whorls, flatter flanks, and an angular venter. At the adoral end of the largest paratype (Pl. 54, fig. 7,8), which appears to be virtually free from distortion, the conch is about 195 mm. high and 90 mm. wide, and the dorsal impressed zone is some 65 mm. deep.

A few of the specimens are silicified, and in them a replacement of the test retains the growth lines. These are fine and inconspicuous, and they form broad rounded lateral salients and a moderately deep ventral sinus.

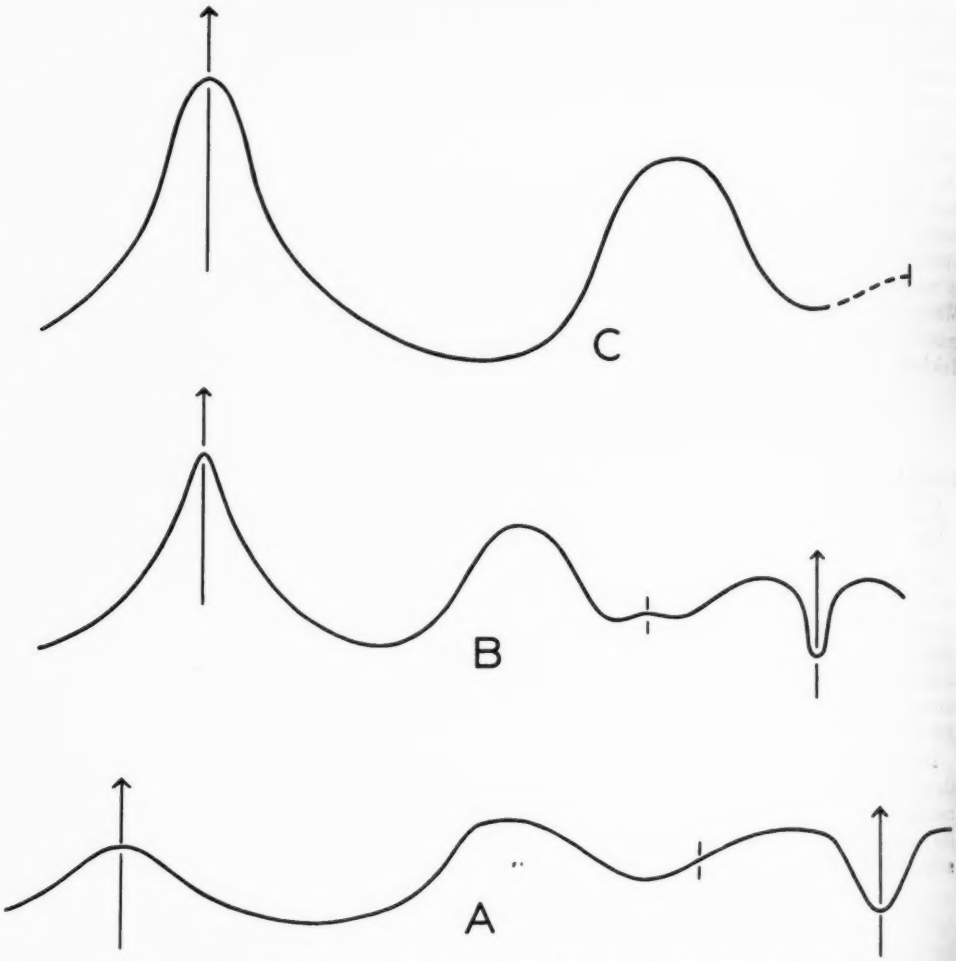
The umbilicus is small and appears to have been nearly closed by an umbilical callus. The umbilical margins are rounded and indefinite.

In moderate to large specimens there are 20 to 25 septa to the volution. Each suture forms a high subangular ventral saddle and on either side of it a broad rounded asymmetrical lateral lobe, a rounded lateral saddle, an umbilical lobe divided by a small low saddle centering on the umbilical seam, and an asymmetrical rounded internal lateral saddle, which extends to the relatively deep narrow rounded dorsal lobe.

The siphuncle is subcentral and is moderately large, its diameter being equal to about a twentieth the height of the conch. It is orthochoanitic in structure, with short septal necks and slightly expanded connecting rings. The latter appear to be unusually sub-



TEXT-FIG. 3—Cross sections of **(A)** the type species of *Deltoidonautilus*, *D. sowerbyi* (Wetherell), from the Lower Eocene London clay, ×$\frac{3}{4}$ (after Edwards); and **(B)** the holotype of *Teichertia prora*, n. sp., ×1.



TEXT-FIG. *4*—Sutures of **(A)** a representative species of *Deltoidonautilus*, from the Upper Cretaceous of Arabia, at a conch height of about 65 mm., ×1; and **(B, C)** early and late mature stages of *Teichertia prora* at conch heights of about 55 mm. and 165 mm., ×1 and ×½, based on the holotype and on paratype 1703, respectively.

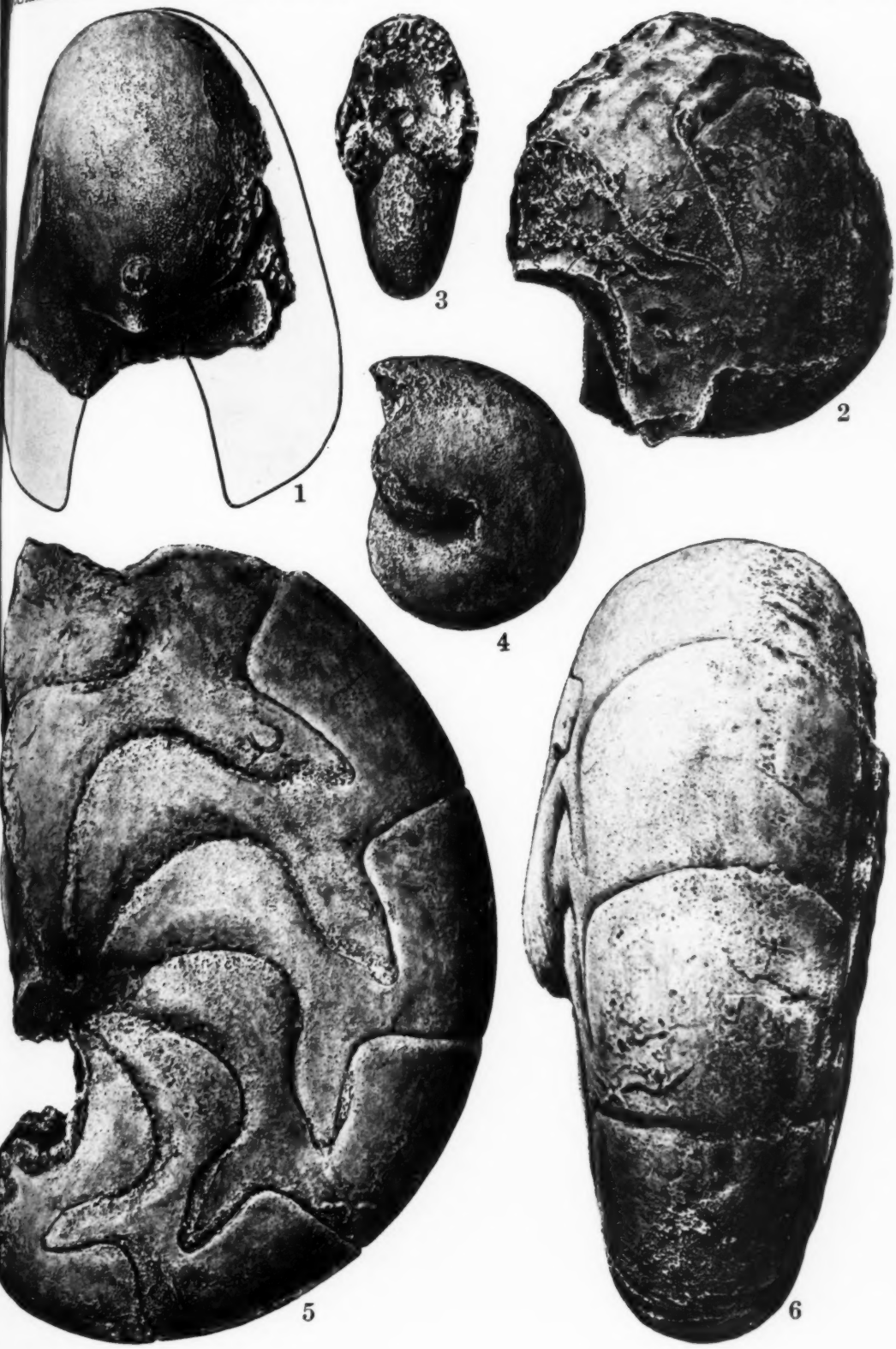
stantial and are therefore readily preserved.

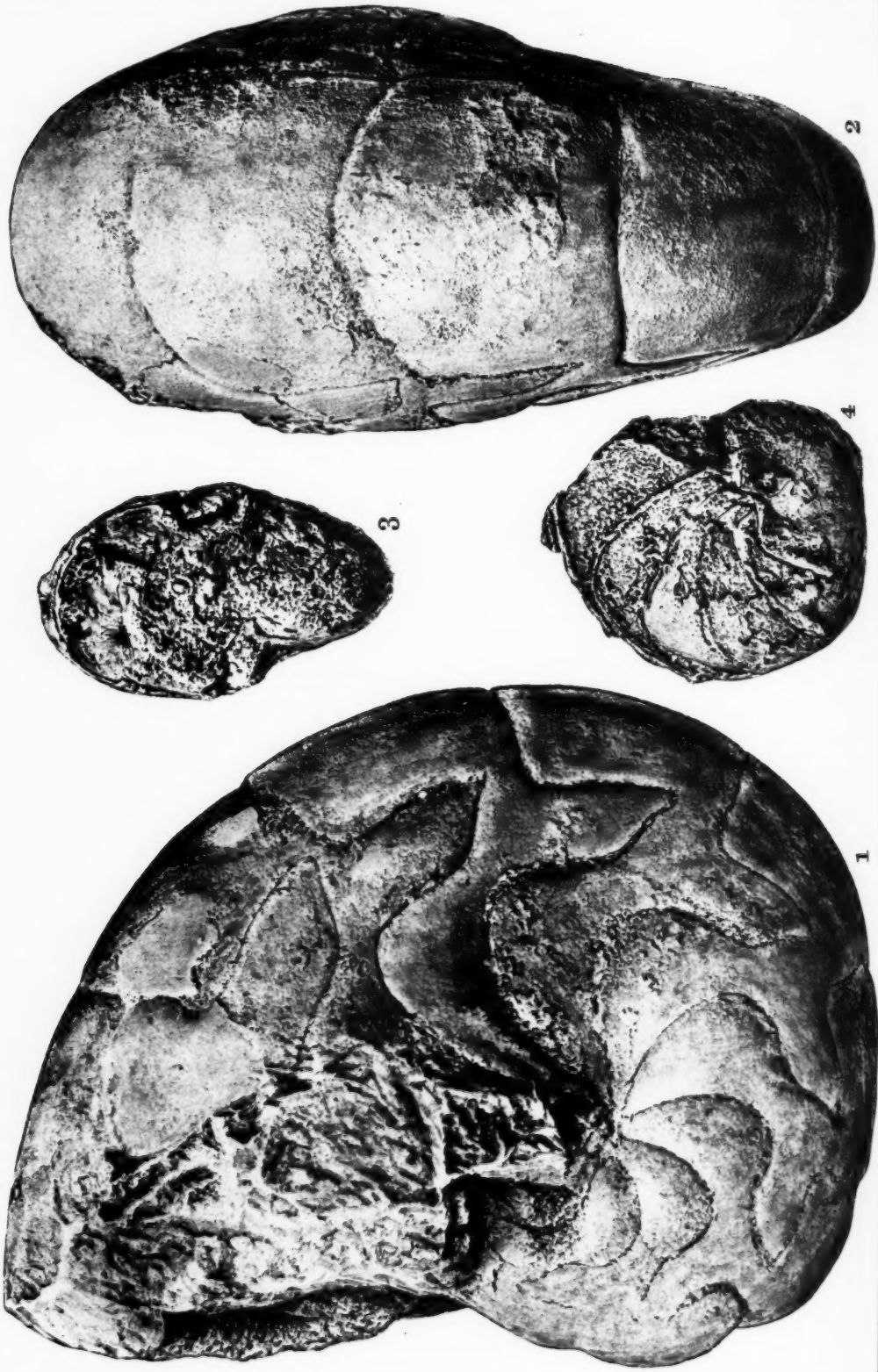
Remarks.—This species resembles certain of the described representatives of *Deltoidonautilus* with angular or subangular venters. However, in at least some of them the angularity is a result of distortion during preservation, whereas even the uncrushed inner whorls of the form under consideration are angular. The prominence of the sutural flexures in our species also differentiates it

EXPLANATION OF PLATE 55

FIG. *1,2,5,6*—*Aturoidea brunnschweileri*, n. sp. *1,2*, paratype (1705) from the Middle Eocene Jubilee calcarenite of One Tree Hill, Western Australia, ×⅔; *5,6*, paratype (1704) from the middle Eocene Giralia calcarenite of the Giralia Range, Western Australia, ×1. (p. 500)

3,4—*Aturia* cf. *A. clarkei* Teichert. A specimen (1713) from the Middle Eocene Giralia calcarenite of the Giralia Range, Western Australia, ×1¼. (p. 502)


1
2
3
4
5
6



from *Deltoidonautilus*. Except for the angular ventral saddle, the general shape of the suture is reminiscent of *Hercoglossa*. As suggested by our synonymy, Teichert regarded this form as being "somewhat intermediate between true *Hercoglossa* and *Deltoidonautilus*."

Occurrence.—The 15 type specimens were collected from the Giralia calcarenite and the Jubilee calcarenite of the Giralia anticline. Most of them (including all those figured) came from the Giralia calcarenite immediately to the south of the Giralia-Bullara road, 2 miles east of the Bullara Station boundary (GIR–2). However, two fragments are labelled as having come from a reddish-brown sandy bed in the underlying Jubilee calcarenite at the top of One Tree Hill, which is nearby. Condon reports that the prolific associated fauna of the Giralia calcarenite places the formation in the "a" to "b" stages (van der Vlerk, 1948) of the East Indies succession, which van Bemmelen (1949) stated to be of probable Middle to Upper Eocene age. However, Brunnschweiler (personal communication) has determined this fauna to be Lutetian (Middle Eocene). Condon considers the Jubilee calcarenite to be uppermost Paleocene, but Brunnschweiler places is also in the Lutetian.

Repository.—Commonwealth of Australia Bureau of Mineral Resources, Canberra. Holotype, catalogue no. 1700; figured paratypes, 1701–1703, and unfigured paratypes, 1704, 1708.

Genus ATUROIDEA Vredenburg, 1925
Type species: *Nautilus parkinsoni* Edwards, 1849

Representatives of this genus are known from all the continents except Antarctica but for the most part are rare, exceptions being *A. olssoni* Miller of the Peruvian Eocene and one of the Australian forms described herewith. The conch is large, attaining a diameter of some 350 mm. in several species. It is thickly subdiscoidal, being broadly rounded ventrally and flattened laterally. The whorls are about as wide as high. The umbilicus is closed, and its margins are indefinite. The test bears no prominent ornamentation.

Each sutures forms five lobes. The ventral saddle is broad and flattened. The adjacent lateral lobes are deep, narrow, and asymmetrically attenuate. The lateral saddles (both internal and external) and the intervening umbilical lobe are rounded. The dorsal lobe is deep and narrow and has parallel flanks. There are some 9 to 12 camerae to the volution.

The siphuncle is subcentral, being close to the dorsum (the bottom of the impressed zone). It is relatively large and has a diameter of about a twelfth the conch height. In structure the siphuncle is hemichoanitic as the septal necks are about half as long as the camerae and the connecting rings extend apicad well past the subjacent septal foramina.

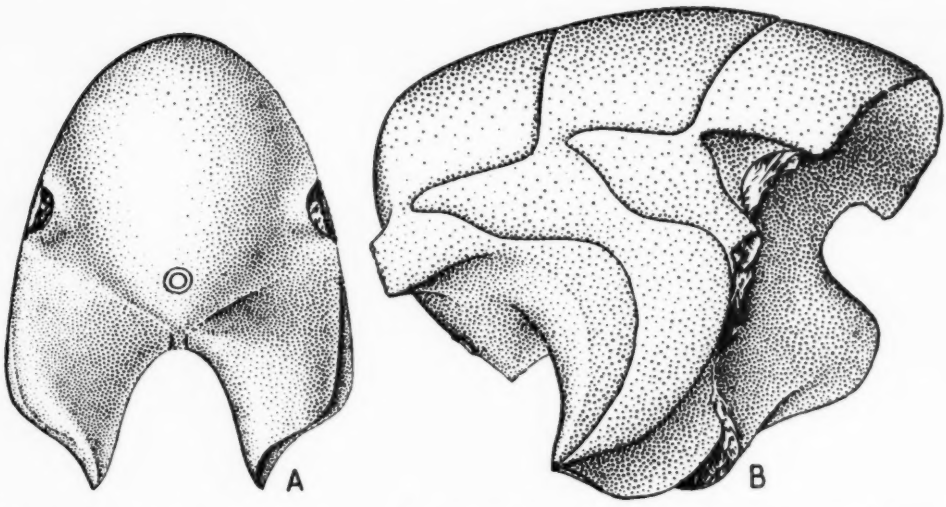
Aturoidea is intermediate between *Hercoglossa* and *Aturia*, and we know transitional forms which link the three genera. *Aturoidea* differs from *Aturia* in that its conch is broader, has fewer camerae per volution, and has a siphuncle that is not marginal and possesses shorter septal necks. *Hercoglossa* characteristically lacks the narrowly rounded junction between the flattened ventral saddle and the lateral lobes, has broader rounded lateral lobes and a broad dorsal lobe with divergent flanks; furthermore, in that genus there is a relatively small orthochoanitic siphuncle, which is generally closer to the venter than to the base of the impressed zone. *Nautilus serpentinus* Blanford and *N. schweinfurthi* Zittel, both Upper Cretaceous in age, are intermediate in development. These species are best regarded as primitive representatives of *Aturoidea*.

The type of *Aturoidea* is from the Lower

EXPLANATION OF PLATE 56

FIG. *1,2—Aturoidea brunnschweileri*, n. sp. Holotype (1707) from the Middle Eocene Giralia calcarenite of the Giralia Range, Western Australia, ×⅔. (p. 500)

3,4—Aturoidea sp. A specimen (1711) from the Paleocene Boongerooda greensand of Scrubby Range, a hill about 20 miles east of Maud Landing, Western Australia, ×1⅓. (p. 501)



TEXT-FIG. 5—Two views of the holotype of the type species of *Aturoidea*, *A. parkinsoni* (Edwards) from the Lower Eocene clay at Harwich, England, ×⅓. Redrawn from Edwards.

Eocene London clay. Congeneric forms are known from the Lower and Middle Eocene, and a few primitive species have been described from the Upper Cretaceous. Geographically, the genus is widespread, having been recorded from England, Austria, Egypt, Angola, India, eastern and western Australia, Peru, and the Atlantic and Pacific coastal regions of the United States.

ATUROIDEA BRUNNSCHWEILERI, n. sp.
Pl. 55, fig. 1,2,5,6; Pl. 56, fig. 1,2

Aturoidea sp. TIECHERT, 1952, Jour. Paleont., vol. 26, p. 737; CONDON, 1954, Australia Bur. Min. Res., Rept. 15, p. 117.

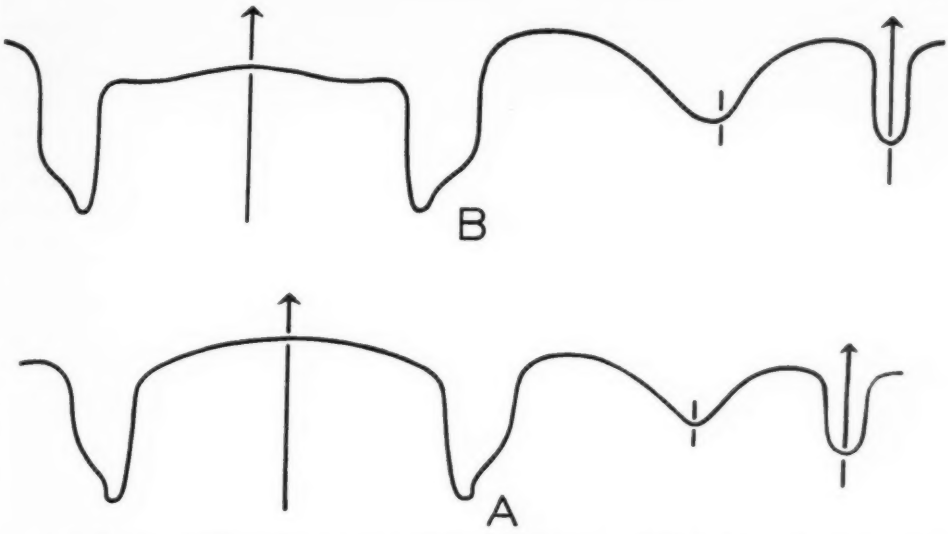
This species is based on eight specimens from the Middle Eocene limestones of the Giralia Range. Though most of them consist exclusively of internal molds of portions of the phragmocone, the holotype is more nearly complete and represents also the adapical portion of the body chamber. The majority of the specimens are composed of yellowish brown calcarenite with scattered grains of glauconite, but some of the paratypes retain silicified portions of the test.

The holotype (Pl. 56, fig. 1, 2), which is virtually undistorted, has an overall measurement of about 210 mm., and near its adoral end its conch is some 135 mm. high and has a maximum width of about 110 mm. It may be presumed that the body chamber was about half a volution long and that this individual, when complete, attained a diameter of nearly 350 mm. Some of the paratypes represent portions of specimens almost a third larger than the holotype.

In the adoral volution of the phragmocone of the holotype, there are 11 camerae. The shape of the sutures is represented by Textfigure 6B. The ventral saddle is flattened and somewhat sinuous. The dorsal lobe is relatively deep and narrow.

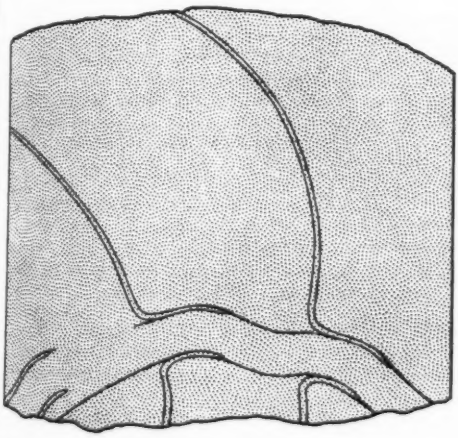
As in congeneric forms, the siphuncle is moderately large. Where the distance between the venter and the bottom of the impressed zone measures some 85 mm., the siphuncle is about 9½ mm. in diameter and its center is some 17 mm. from the bottom of the impressed zone. A section through the siphuncle of a paratype shows that the septal necks are about half as long as the camerae and follow the curvature of the shell. The connecting rings, though somewhat indistinct, appear to be cylindrical; they overlap the adapical portion of the septal necks and invaginate into the preceding septal foramina.

Remarks.—This form closely resembles the type species of the genus, *A. parkinsoni* (Edwards). In both, the junctions of the ventral saddle with the lateral lobes are narrowly rounded, the ventral saddle is somewhat sinuous, and the dorsal lobe is narrow and has straight parallel sides. These two forms are advanced representatives of



TEXT-FIG. 6—Sutures of **(A)** *Aturoidea vieirai* Miller from Angola and **(B)** *A. brunnschweileri*, n. sp.. from Western Australia, both ×½. The former is relatively primitive but is about average for the genus *Aturoidea*.

Aturoidea. They differ from the postgeniture, *Aturia*, in that their conchs are broader, their camerae are longer, their sutures have wider less acute lateral lobes and a dorsal lobe that is not contracted adorally, and their siphuncle is not marginal and has shorter septal necks. *Aturoidea distans* Teichert from southeastern Australia differs from the Western Australian species in that the lateral lobes of its sutures are relatively long, narrow, and pointed.



TEXT-FIG. 7—Diagrammatic representation of a longitudinal section through the siphuncle of *Aturoidea brunnschweileri*, n. sp., based on a paratype (1709), ×¾.

Occurrence.—All eight of the type specimens came from the Giralia Range of Western Australia. The holotype is from 3 feet above the base of the Giralia calcarenite 12 miles ENE of Bullara Homestead, about the same distance WNW of Giralia Homestead, and 1¾ miles SSE of Jubilee Bore (GIR-1). Two of the paratypes (1706, 1710) are from a dense yellowish brown limestone member of the same formation 6½ miles south of Jubilee Bore (GIR-3). The other paratypes are from a reddish brown sandy limestone in the Jubilee calcarenite near the top of One Tree Hill, where they are associated with *Teichertia prora* n. sp.

Repository.—Commonwealth of Australia Bureau of Mineral Resources, Canberra. Holotype, catalogue no. 1707; figured paratypes, 1705, 1706, 1709; and unfigured paratypes, 1710, 1718.

ATUROIDEA sp.
Pl. 56, fig. 3,4

Aturoidea sp. TEICHERT, 1952, Jour. Paleont., vol. 26, p. 737; CONDON, 1954, Australia Bur. Min. Res., Rept. 15, p. 117.

Two relatively small specimens from the lowermost Paleocene of Western Australia appear to represent *Aturoidea* but are so in-

complete that they can not be identified specifically. Both are only some 40 mm. in diameter, but they preserve on the outer surface the internal sutures of a succeeding volution. These indicate that the phragmocone attained an overall measurement of at least 100 mm.

Near the adoral end of the figured specimen, the maximum height and width of conch are subequal and measure a little more than 25 mm. The umbilicus is small and inconspicuous and is filled by a callus. The growth lines are fine and form a moderately deep ventral sinus and broad rounded lateral salients. The test is silicified, but the remainder of both specimens is calcareous.

The shape of the external suture is not revealed. The internal suture consists of a deep narrow dorsal lobe, which is about a third as wide as deep, has straight parallel sides, and is similar to that of *A. brunnschweileri*, just described. The internal lateral saddles are also similar to those of that species. Where the overall measurement of the unfigured specimen is about 42 mm., the siphuncle is a little more than 2 mm. in diameter and its center is some 3 mm. from the bottom of the impressed zone.

Remarks.—Although only the internal sutures of this form are known, their shape, together with the position of the siphuncle, are sufficient for generic identification. Detailed comparisons with other species of *Aturoidea* are not possible, because only large representatives of them have been described. However, the siphuncle of the specimens under consideration is proportionately small.

Occurrence.—Boongerooda greensand (lowermost Paleocene) of Scrubby Range, a hill 19½ miles ESE of Maud Landing and 33½ miles WSW of Winning Pool, Western Australia.

Repository.—Commonwealth of Australia Bureau of Mineral Resources, Canberra. Figured specimen, catalogue no. 1711; unfigured specimen, 1712.

Genus ATURIA Bronn, 1838
Type species: *Nautilus Aturi*
Basterot, 1825

ATURIA cf. A. CLARKEI Teichert
Pl. 55, fig. 3,4

Five fragments of aturias have been collected from the Middle Eocene Giralia calcarenite in the Giralia Range. They indicate that the species which occurs there attains a diameter of at least 100 mm. and that its whorls are about three-fourths as wide as high. Their general physiognomy and proportions suggest a relationship to *Aturia clarkei* Teichert, originally described from the Eocene of the Kennedy Range, some 125 miles to the southeast. The relative measurements of at least the figured specimen and a somewhat larger individual are almost exactly proportional to those given by Teichert for the holotype of his species. *A. australis* McCoy, first described from the Lower Miocene and late Oligocene of southeastern Australia, has narrower whorls.

Occurrence.—Giralia calcarenite immediately south of the Giralia-Bullara road, 2 miles east of the Bullara Station boundary (GIR-2), Western Australia; in association with *Teichertia prora*, n. sp., and *Aturoidea brunnschweileri*, n. sp.

Repository.—Commonwealth of Australia Bureau of Mineral Resources, Canberra. Figured specimen, catalogue no 1713; unfigured specimens, 1719.

BIBLIOGRAPHY

BASTEROT, B. DE, 1825, Description géologique du bassin Tertiaire du sud-ouest de la France, première partie, comprenant les observations générales sur les Mollusques fossiles, et la descriprion particulière de ceux qu'on recontre dans ce bassin: Paris Soc. Hist. Nat., Mém., t. 2, 100 p., 7 pl.

BEMMELEN, R. W. VAN, 1949, The geology of Indonesia; vol. IA, general geology of Indonesia and adjacent archipelagoes, xxiii+732 p.

BRONN, H. G., 1838, Lethaea geognostica ..., Bd. 2, p. 769–1346.

CHAPMAN, FREDERICK, & CRESPIN, IRENE, 1934, The palaeontology of the Plantagenet beds of Western Australia: Roy. Soc. West. Australia, Jour., vol. 20, p. 103–136, pl. 6–11.

CONDIT, D. D., RAGGATT, H. G., & RUDD, E. A., 1936, Geology of Northwest Basin, Western Australia: Am. Assoc. Petrol. Geol., Bull., vol. 20, p. 1028–1070.

CONDON, M. A., 1954, Progress report on the stratigraphy and structure of the Carnarvon Basin, Western Australia: Comm. Australia Bur. Min. Res., Rept. 15, iv+163 p., 3 pl.

CONRAD, T. A., 1866, Observations on Recent and fossil shells, with proposed new genera and species: Am. Jour. Conch., vol. 2, p. 101–103.

EDGELL, H. S., 1952, The micropalaeontology of the Giralia Anticline, North-West Australia: Comm. Australia Bur. Min. Res., Rec. 1952/75 (unpublished).

EDWARDS, F. E., 1849, A monograph of the

Eocene Mollusca; or description of shells from the older Tertiaries of England; Part 1, Cephalopoda: Palaeontographical Soc., vol. 2, p. 1–56, pl. 1–9.

GALEOTTI, M. H., 1837, Mémoire sur la constitution géognostique de la province de Brabant, en réponse à la question suivante; décrire la constitution géologique de la province de Brabant, déterminer avec soin les espèces minérales et les fossiles que les divers terrains renferment et indiquer la synonymie des auteurs qui en ont déja traité: Mém. couronnés l'Acad. Roy. Sci. Bel.-Lett. Bruxelles, t. 12, 192 p., 4 pl.

GLAESSNER, M. F., 1955, Pelagic fossils (aturia, penguins, whales) from the Tertiary of South Australia: S. Australia Mus., Rec., vol. 11, p. 353–372, pl. 24–26.

JUTSON, J. T., & SIMPSON, E. S., 1916, Principal results of the year's operations; Albany: West. Australia Geol. Surv., Ann. Prog. Rept. for 1915, p. 24.

—— & ——, 1917, Notes on the geology and physiography of Albany: Roy. Soc. West. Australia, Jour. & Proc., vol. 2 (1915-1916), p. 45–48, pl. 1–5.

McCOY, FREDERICK, 1867, On the Recent zoology and palaeontology of Victoria: Ann. Mag. Nat. Hist., ser. 3, vol. 20, p. 175–202.

MILLER, A. K., 1947, Tertiary nautiloids of the Americas: Geol. Soc. Am., Mem. 23, viii+234 p., 100 pl.

—— & CRESPIN, IRENE, 1939, An *Aturia* from the Northwest Division of Western Australia: Jour. Paleont., vol. 13, p. 79–81, pl. 13, 14.

—— & HARRIS, R. A., 1945, North American Cymatoceratidae (Mesozoic Nautiloidea): Jour. Paleont., vol. 19, p. 1–13, pl. 1–5.

NEWTON, R. B., 1919, On a sandstone cast of *Aturia aturi* (Basterot) from the Miocene of Western Australia: Malac. Soc. London, Proc., vol. 13, p. 160–167, pl. 5,6.

TEICHERT, CURT, 1944, The genus *Aturia* in the Tertiary of Australia: Jour. Paleont., vol. 18, p. 73–82, pl. 14–16.

—— & GLENISTER, B. F., 1952, Fossil nautiloid faunas from Australia: Jour. Paleont., vol. 26, p. 730–752, pl. 104–108.

VLERK, I. M. VAN DER, 1948, Stratigraphy of the Cainozoic of the East Indies based on Foraminifera: Internat. Geol. Congr., 18th. Sess., Proc. Internat. Palaeont. Union, p. 61–63.

VREDENBURG, E. W., 1925, Descriptions of Mollusca from the post-Eocene Tertiary formation of north-western India; Cephalopoda, Opisthobranchiata, Siphonostomata: India Geol. Survey, Mem., vol. 50, pt. 1, p. 1–350, pl. 1–13.

MANUSCRIPT RECEIVED JANUARY 9, 1956

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 504–520, PL. 57–60, 4 TEXT-FIG., MAY 1956

TYPE AND OTHER SPECIES OF ODONTOPLEURIDAE (TRILOBITA)

HARRY B. WHITTINGTON
Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts

ABSTRACT—The type and other species of six genera, and two typical species of a seventh genus of odontopleurids are described. Much new morphological information has been obtained, and has modified previous concepts of the genera and their relationships. All illustrations are new. *Leonaspis* is diagnosed, *L. tuberculatus* and a new Oklahoma species, *L. williamsi*, is described; reasons are given for believing that the characters on which two subgenera of *Leonaspis* have recently been erected are of doubtful value. New information on *Acidaspis*, including the nature of the hypostome, is derived from study of *A. brightii* and *A. cincinnatiensis*. Well preserved material of *Dudleyaspis quinquespinosa* suggests that this genus is closely related to *Acidaspis*. A new reconstruction of *Miraspis mira* has been made, and a Lower Devonian species from Oklahoma is described but not named; the genus has a longer range in time than previously supposed. Latex casts of the original material of *Proceratocephala terribilis* show it to be most probably conspecific with "*Acidaspis discreta*," which latter was recently designated type of the genus *Drummuckaspis*. Topotype specimens are used for a revision of *Whittingtonia bispinosa*, and this genus is believed to be closely related to *Ceratocephala*. A new reconstruction of *Dicranurus monstrosus* shows the cephalon in correct relation to the rest of the exoskeleton; the genus is discussed and new material of the type species from Oklahoma described. The spinyness of the odontopleurid exoskeleton has been used as evidence for a probable floating habit, but it is shown that the exoskeleton is specially adapted for resting in a particular attitude on a flat surface.

INTRODUCTION

IN 1949 F. Prantl and A. Přibyl published their study of odontopleurid trilobites (English text p. 119–221, to which all references given herein apply), based largely on the collections of the National Museum of Prague, but also on some type and topotype material from extra-Bohemian areas. These authors raised this group to the rank of superfamily, dividing it into three families and various subfamilies. Nine new genera were erected (four on English, Scottish, and Irish species) but neither all of these, nor all the older genera, were exactly placed in their scheme. Erben (1952) suggested modifications of part of Prantl & Přibyl's classification.

At about the time Prantl & Přibyl's work appeared I had begun the study of a large collection of silicified Middle Ordovician odontopleurids from Virginia. Two species from this collection have been described (Whittington & Evitt, 1954), and descriptions of the remaining fourteen species are now in press. A great deal of new information on morphology, ontogeny, and evolution of odontopleurids has been accumulated. In addition I have had the opportunity to examine the type species of genera founded on British material, as well as Bohemian specimens in the Museum of Comparative Zoology, and collections in the U. S. National Museum and other centers. Study of these old species shows that previous descriptions and illustrations are inadequate, and provide an erroneous basis on which to erect new genera. The most striking examples of this are the Scottish Starfish bed specimens described by Reed as two different species, each of which was made the type of a new genus by Prantl & Přibyl. There seems little doubt but that all of the material except an isolated pygidium is of one species. The following pages, then, are intended to provide more adequate figures and descriptions of these old species, and thus to provide a better understanding of certain genera. In addition, three species are described, based on the exceptionally fine material collected by Dr. G. Arthur Cooper and his associates from the Lower Devonian Haragan shale of Oklahoma. The odontopleurids are here regarded as constituting a family (cf. Whittington & Evitt, 1954, p. 52–53), and, while comments are made on the relations between certain

genera, subfamilies are not used. A revision of odontopleurid systematics, incorporating all the new information, will accompany the description of the silicified material. Terminology of descriptions and orientation of the exoskeleton follows that of Whittington & Evitt (1954, p. 11–14) except that I have preferred the term "librigenal" (Richter, 1932) for the spine at the posterolateral corner of the cheek.

The following persons have generously helped me by permitting study of material in their charge, making loans, and supplying data:—

Mr. R. Baker, British Museum (Natural History) London (BM); Dr. G. Arthur Cooper, U. S. National Museum, Washington, D.C. (USNM); Mr. A. G. Brighton, Sedgwick Museum, Cambridge, England (SM); Dr. Ethel D. Currie, Hunterian Museum, Glasgow, Scotland, (HM); Mr. F. D. Holland, Jr., University Museum, Cincinnati; Dr. V. Jaanusson, Paleontological Institute, Uppsala, Sweden; Mr. Clinton F. Kilfoyle, New York State Museum, Albany (NYSM); Dr. I. Strachan, Geological Museum, Birmingham University, England (BU); initials in brackets are used subsequently to indicate the whereabouts of particular specimens. I am grateful for a grant from the Shaler Memorial Fund, Harvard University, which enabled me to visit Europe in 1953. In London Mr. W. H. C. Ramsbottom, Geological Survey and Museum, helped me to make both latex casts and photographs. Mrs. Robert E. Kay, Mrs. Stanley J. Olsen and Mr. Ira B. Laby have prepared the enlargements from my negatives, and Miss Pat Washer made the drawings.

MODE OF LIFE OF ODONTOPLEURIDAE

In *Acidaspis* and *Dudleyaspis* there is a row of almost vertically-directed spines on the antero-lateral cephalic border (Text-fig. 1,2; cf. Pl. 58, fig. 12,16). These spines are graduated in length so that the cephalon will rest on a flat surface on their tips and the anterior cephalic margin, as shown in the drawings, and the posterior margin of the occipital ring is approximately vertical. The thorax and pygidium, if stretched out roughly parallel to this surface, would lie a short distance above it. It is evident that a similar position is possible for *Miraspis* (Text-fig. 3). In *Dicranurus* (Text-fig. 4) and *Ceratocephala* (Whittington & Evitt, 1954, text-fig. 14) a like attitude is attained by the antero-lateral extension of the free cheeks rather than by spines. In *Whittingtonia* (Pl. 59, fig. 4,8) the cheeks show a combination of both structures. In *Leonaspis* (Pl. 57, fig. 13,14) the cephalon is less convex, but spines along the antero-lateral margin of the cephalon support it in the same position. It thus seems that odontopleurids of diverse form were all adapted to rest close to the sea floor in approximately the same attitude. A possible reason for this adaptation is that it was a feeding position, in which movements of the appendages created currents carrying food particles to the mouth. Other trilobites, of quite different types—e.g., Harpidae (Whittington, 1950, p. 25–26), Bathyuridae (Whittington, 1953, p. 651, text-fig. 1), some illaenids and cheirurids—could rest on the sea bottom in the same attitude. Most students have, however, regarded odontopleurids as floating in habit, because of the spinyness of the exoskeleton and the wide and seemingly rapid geographical distribution (Prantl & Přibyl, 1949, p. 132, 209; Whittington & Evitt, 1954, p. 32–33 and references). The floating larval stages may account for the distribution, and the spines, while they inhibit sinking, may also have a protective as well as a balancing function. Thus it seems that while odontopleurids may have drifted (or swum feebly?) in some region of the sea, they also, like many other trilobites, spent considerable periods resting on a more or less flat surface, presumably the sea bottom.

SYSTEMATIC PALEONTOLOGY

Family ODONTOPLEURIDAE Burmeister, 1843

Genus LEONASPIS R. & E. Richter, 1917

Acanthaloma CONRAD, 1840. R. & E. RICHTER, 1952, regard as undesirable the revival of Conrad's name *Acanthaloma* (Prantl & Přibyl, 1949, p. 151). I am in agreement with them, and have submitted a proposal for the suppression of this name to the International Commission on Zoological Nomenclature.

pe species.—Odontopleura leonhardi Barrande 1846.

Diagnosis.—Glabella as wide across large basal glabellar lobes as across occipital ring, two pairs glabellar lobes, the anterior smaller than the basal, occipital ring not greatly lengthened or inflated, median tubercle or short median spine. Eye lobe opposite posterior part of basal glabellar lobe of occipital furrow, large to medium size, two branches of suture almost at right angles adjacent to eye lobe, cross border furrows on sutural ridges. Librigenal spine broad-based. Thorax of 8–10 segments, pleurae with anterior pleural spines short, may be bifid distally, posterior band continuous with stout posterior pleural spine; anterior two or three segments may be facetted and pleural spines reduced. Pygidium usually with prominent pair border spines, one or two pairs small border spines between them.

Geological range.—Lower Silurian to Middle Devonian.

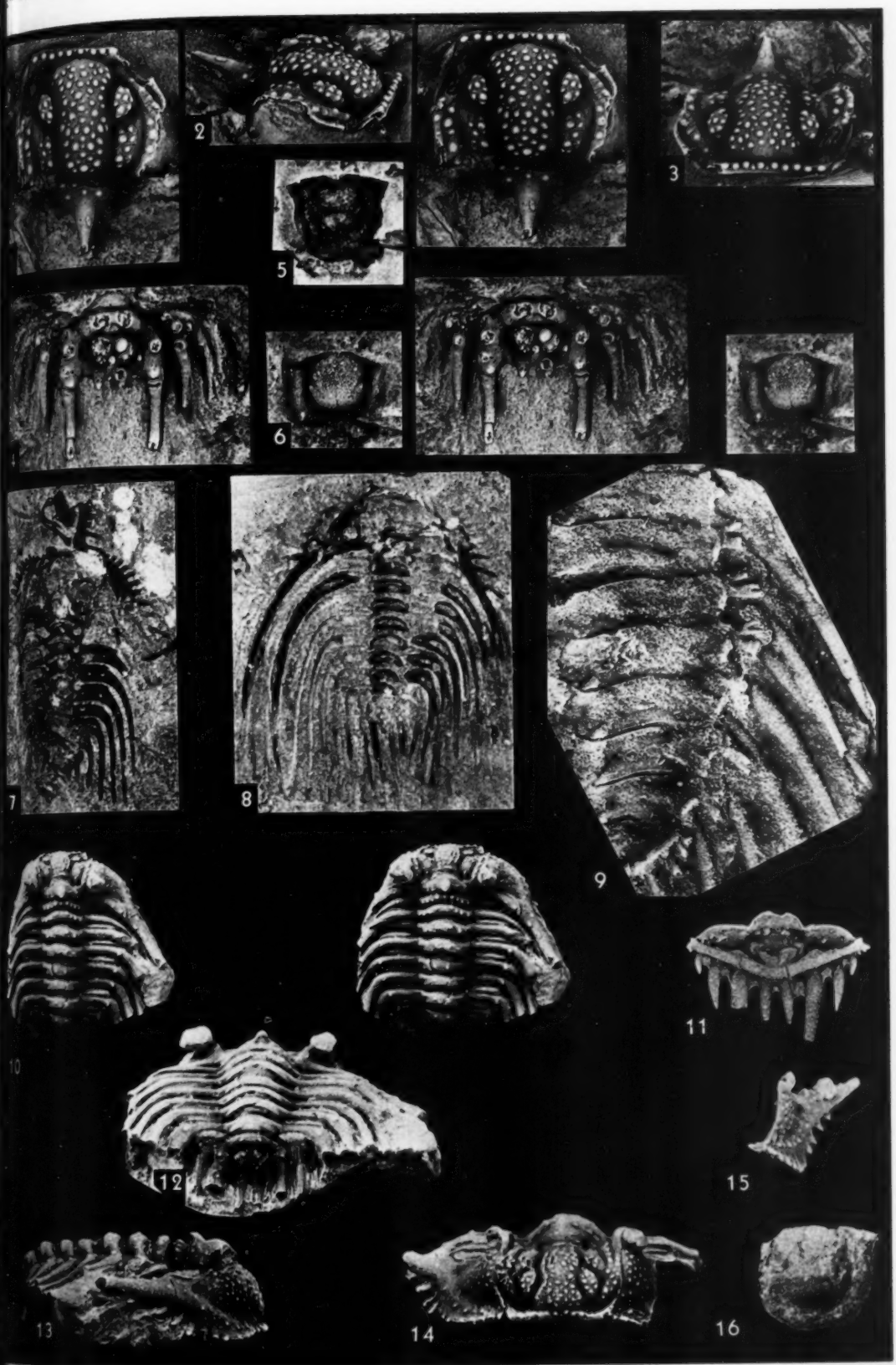
Discussion.—Prantl & Přibyl (1949, p. 164–171) distinguished two subgenera of *Leonaspis* (*"Acanthaloma"*)—namely *Acanthalomina* and *Kettneraspis*. The former was characterized by shape of cephalon, presence of spines on axial and pleural regions of thorax and pygidium, lack of anterior pleural spines, and absence of ridge on pleural lobe of pygidium. Examination of topotype specimens of the type species, *L. minuta* (Barrande), shows that small outwardly and downwardly directed anterior pleural spines are present on the thorax, and that a low ridge runs from opposite the first axial ring of the pygidium out to the base of the major border spine. Thus we are left with only cephalic shape and ornament of thorax and pygidium to distinguish this subgenus, and both these characters seem of doubtful value for this purpose. *Kettneraspis* was distinguished particularly by the so-called "stunting" of the first two thoracic segments. These segments are not notably shorter (sag. and exs.) than those following, but are cut off anterolaterally by the facet so that there seems to be no anterior pleural spine, and only a short posterior pleural spine. This facetting enables these first two segments to fit beneath the librigenal spine, and the same type of facetting is seen in *L. williamsi*, n. sp. (Pl. 57, fig. 10). A progressive type of facetting is seen on the first three segments of *L. coronata* (Salter, 1853) (Pl. 59, fig. 12). Thus the facetting seems to be variable, and of itself scarcely sufficient to distinguish a subgenus, but I have not had the opportunity to study material of the type species [the holotype of *L.* (*Kettneraspis*) *pigra*, said by Prantl & Přibyl (1949, p. 168) to be in the Museum of Comparative Zoology collections, has not been found]. Thus, because of their questionable value, I have not used these subgenera, and would include in *Leonaspis* a greater variety of species than did Prantl & Přibyl—for example, both *L. coronata* and *L. deflexa* (Lake, 1896) from the English Wenlock limestone. Prantl & Přibyl (1949, p. 146, 167) excluded these species from *Leonaspis* because of the presence of 10 thoracic segments and the broad librigenal spine. The number of thoracic segments appears to vary (*L. williamsi*, n. sp., has eight) and the stoutness of the librigenal

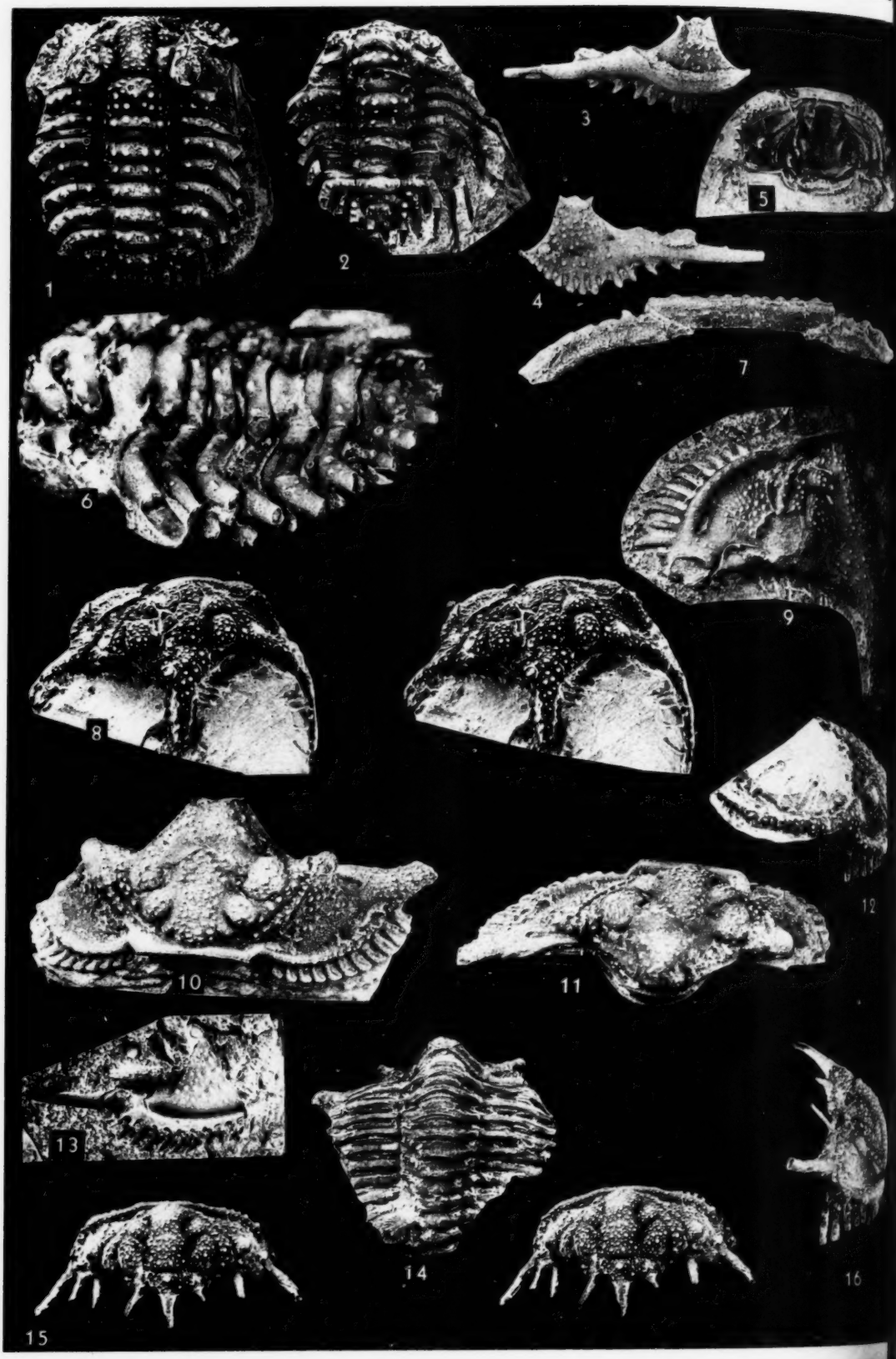
---

EXPLANATION OF PLATE 57

FIG. *1–9*—*Leonaspis tuberculatus* (Conrad), New Scotland limestone, Albany or Schoharie county, New York, *1,2,3*, incomplete cranidium, exterior stereograph, right lateral, anterior views, original of Hall, 1861, pl. 79, fig. 3,5; ×3, NYSM 4198. *4*, pygidium, exterior stereograph, original of Hall, 1861, pl. 79, fig. 14; ×3, NYSM 4200. *5,6*, hypostome, exterior view, photographed under alcohol, exterior stereograph, ×6, NYSM 10704. *7,8*, incomplete specimen, counterparts, photographed under alcohol, original of Hall, 1861, pl. 79, fig. 1,1a; ×3, NYSM 4196, 4197. *9*, part of thorax and pygidium, exposed from ventral side, ×4½, NYSM 10705, from Clarksville, Albany county, New York.

10–16—*Leonaspis williamsi*, n. sp., Haragan shale, Arbuckle Mountains, Oklahoma. *10,12-14*, holotype, almost complete exoskeleton, dorsal stereograph, ×2, posterior, right lateral, anterior views, ×3. White Mound. USNM. *11*, pygidium, ventral view, ×4. Near Old Hunton. USNM. *15*, free cheek, anterior view, ×4. Near Old Hunton. USNM. *16*, hypostome, exterior view, ×6. White Mound. MCZ 5262.


2
3
5
6
7
8
9
10
11
12
13
14
15
16


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

spine hardly seems sufficient of itself to distinguish these species.

LEONASPIS TUBERCULATUS (Hall, 1859)
Pl. 57, fig. 1–9

Acidaspis tuberculatus HALL, 1859–61, p. 368–370, pl. 79, fig. 1–14.

Authorship of species.—Conrad (1840, p. 205) proposed the name *Acanthaloma* for a free cheek found near Clarksville, N. Y., and gave a description. On the same page he also proposed the name *Acidaspis tuberculatus* for a trilobite cephalon from the same locality, and gave a description. The next year Conrad (1841, p. 31) listed the name *Acantholoma* (an erroneous subsequent spelling), and on page 39 of the same paper listed *Acidaspis tuberculatus* and *Acantholoma spinosa* (new name). No reference was made to the earlier report. Castelnau (1843, p. 23) later proposed the name *Acantholoma conradi*, referring to Conrad's 1840 paper and mentioning the locality. The whereabouts of Conrad's specimens are unknown, but it seems clear from the brief descriptions that all the names mentioned above, with the possible exception of *A. spinosa*, refer to one species. The New Scotland beds in the neighborhood of Clarksville gave a collecting ground well known to the early workers (Ruedemann, 1930, p. 49), and Hall (1859–61) was the first to give a full, illustrated description of *Acidaspis tuberculatus* from these beds. His specimens are preserved in the New York State Museum, and are the only authority for the species. I think we should accept it from Hall, and in my appeal for the suppression of the name *Acanthaloma* by the International Commission on Zoological Nomenclature I am therefore asking that both Conrad's and Castelnau's specific names be rejected.

Syntypes.—(see Clarke & Ruedemann, 1903, p. 670) NYSM 4198, incomplete cranidium, original of Hall, 1861, pl. 79, fig. 3, 5; NYSM 4196, 4197, counterparts of incomplete specimen, original of Hall, 1861, pl. 79, fig. 1,1a; NYSM 4199, part of thorax and pygidium exposed from under side, original of Hall, 1861, pl. 79, fig. 12; NYSM 4200, pygidium, original of Hall, 1861, pl. 79, fig. 14; all from New Scotland limestone, Helderberg stage, Lower Devonian, Albany (or Schoharie) County, New York.

In the American Museum of Natural History, no. 2615/1, are the originals of Hall, 1861, pl. 79, figs. 6, 8, 8a, 9, and 10. These are all free cheeks, of the same type as those described below, and four additional specimens of free cheeks are included in this lot. These specimens, loaned to me through the kindness of Dr. Donald F. Squires, were not examined until this paper was in press. However, they are of minor importance in characterizing the species and add no new information to that given below.

Other Material—NYSM 10705, an incomplete specimen exposed from the ventral side; New Scotland limestone, near Clarksville, Albany County, N.Y. NYSM 10704, a slab showing a hypostome and two cranidia, same horizon, Schoharie County, N.Y.,

---

EXPLANATION OF PLATE 58

FIG. *1-4,6,7,—Leonaspis williamsi*, n. sp., Haragan shale, Arbuckle Mountains, Oklahoma. *1*, dorsal view, ×3. Vines Dame. USNM. *2,6*, dorsal, ×2, left dorsolateral view, ×4. White Mound. USNM. *3,4*, free cheek, interior and exterior views, ×4. Near Old Hunton. USNM. *7*, anterior cephalic doublure and rostrum of holotype, ×6. White Mound, USNM.

5,15,16—Dudleyaspis quinquespinosa (Lake), Wenlock limestone, Wren's Nest, Worcestershire, England. *5*, interior view of cephalon, ×2. BU 676, Holcroft Collection. *15, 16*, dorsal stereograph of cephalon, ×3, right lateral view, ×5. BU 677, Holcroft Collection.

8,12—Acidaspis brightii Murchison, Wenlock limestone, Wren's Nest, Worcestershire, England. Cephalon, dorsal stereograph, right lateral view, ×2. BU 678, Holcroft Collection.

9-11,13,14—Acidaspis cincinnatiensis Meek. *9*, incomplete cephalon, exterior view, ×2. McMillan formation, Corryville member, Mt. Auburn, Cincinnati, Ohio. USNM. *10,11,14*, partly enrolled incomplete specimen, anterior, dorsal of cephalon, dorsal of thorax, respectively, ×2¼, ×2¼, ×1½. McMillan formation, Corryville member, Cincinnati, Ohio. USNM 43086. *13*, internal mould of free cheek, exterior view, original of Bassler, 1932, fig. 3, ×2. Catheys limestone, upper beds, Rhodes quarry, 1½ miles southwest of Franklin, Tennessee. USNM 78552.

7 slabs with cranidia, free cheeks and pygidium, NYSM, same horizon, Albany and Schoharie counties, N.Y.

Description.—Cranidium (Pl. 57, fig. 1–3) with occipital ring convex, stout median spine directed upwards and backwards, occipital furrow broad, shallow medially, deep in outer portions. Glabella widest at outer ends of basal glabellar furrows; two pairs of lateral lobes, outline ovate (long axis longitudinal). Basal (first) glabellar lobe gently convex, defined anteriorly by basal glabellar furrow which runs straight inward and backward, deepest at inner end, and laterally by broad, shallow axial furrow. Second lateral glabellar lobe smaller than basal, more convex, defined anteriorly by second lateral furrow which is deep and parallel to basal furrow; axial furrow outside second lobe slightly deeper and narrower. Median glabellar lobe half total width, parallel-sided, convex, set off from lateral lobes by deep, broad furrows into which the lateral glabellar furrows run. Median lobe expands forward into frontal lobe, and lateral margin of latter merges into anterior end of eye ridge. Palpebral lobe situated approximately opposite end of occipital furrow, on highest point of narrow fixed cheek. Eye ridge runs in curve convex outward, at first slightly outward, then curving inward to frontal glabellar lobe; not separated from latter by axial furrow. Inside eye ridge narrow (tr.), convex segment of fixed cheek. Anterior branch of facial suture runs forward in curve convex outward, opposite basal glabellar furrow begins to diverge from eye ridge, but still curves inward, and crosses anterior border in line (exs.) with median portion of axial furrow. Between suture and eye ridge a subtriangular segment of fixed cheek is enclosed, widest anteriorly, where the deep anterior pit is situated in the inner corner (Pl. 57, fig. 3). Anterior border short (sag. and exs.), convex, running transversely in straight line. Posterior border and course of posterior branch of suture not preserved. External surface with coarse tubercles on occipital ring, glabellar lobes, eye ridge, fixed cheek inside eye ridge, and in single row on anterior border. Dimensions of cranidium (NYSM 4198) in millimeters: length (sag.) projected about 5.6; length (sag.) of glabella projected about 4.2; maximum width (tr.) glabella 6.3; width cranidium across palpebral lobes 9.8; height cranidium (excluding occipital spine) 6.3.

Free cheek (poorly preserved, see Pl. 57, fig. 7,8) triangular in outline, convex, with gently convex lateral border becoming wider (tr.) posteriorly and merging with the broad base of librigenal spine. Latter long, curved, tapering back and terminating opposite tip of axis of pygidium. Lateral border of free cheek with row of outwardly projecting spines, longest posteriorly, the row extending on to proximal part of librigenal spine. Two or three spines on inside of proximal portion of librigenal spine. Coarse tubercles on cheek and lateral border, not in border furrows. Hypostome (Pl. 57, fig. 5,6) of maximum width across anterior wings 2.6 mm., of length (sag.) 2.2 mm. Middle body convex, subcircular in outline, middle furrows short, shallow, running inward and backward from about half the length. Border furrows broad and shallow. Anterior border shortest (sag.) in mid-line, lateral borders with shallow notch and shoulders not prominent, posterior border long (sag. and exs.) and flattened, sloping gently inwards. A long, thin fragment of a shell lies on this hypostome along the posterior border furrow. The posterior border is therefore slightly damaged, but the photograph taken under alcohol (Pl. 57, fig. 5) shows the position of the posterior margin.

Thorax (Pl. 57, fig. 7–9) of nine segments, axis convex, width about one-third of total. Articulating half-ring of same length as ring. First two segments short (sag. and exs.), third longest, remainder progressively shorter backward. Pleura with broad (exs.), convex median ridge, narrow (exs.) depressed band posterior to ridge, somewhat wider (exs.), low, convex band along anterior margin. Median transverse ridge of pleura extended into posterior pleural spine, those of first two segments short, of third long, tapering and curving back to tip, so that distal part of spine points backward and tip is about level with tip of pygidial spines. Successive posterior pleural spines are similarly shaped and curve back subparallel to the third, and reach to approximately the same point. Anterior transverse ridge of pleura extended into a pair of short

anterior pleural spines (Pl. 57, fig. 9) fused proximally, each of which may bifurcate at the tip. These spines are directed more strongly outwards than the posterior spines, and lie beneath the proximal part of the posterior spine of the segment in front. Two stout tubercles on the median ridge of each pleura, one close to the axial furrow, the other at the fulcrum. Small tubercles on the anterior pleural ridge.

Pygidium (Pl. 57, fig. 4) with axis of two rings, the axial furrow shallow beside the first, a deep pit beside the second and becoming shallow behind it. Pleural region with a strong raised ridge curving out from beside the first axial ring to run directly back into the major border spine. Antero-laterally to this ridge pleural region gently convex. At ventral margin of antero-lateral edge of pygidium two short border spines (Pl. 57, fig. 9) fused at their bases. These spines correspond in form to the anterior pleural spines of the thorax, and at least the anterior is commonly concealed in specimens exposed from the dorsal side. Third and fourth border spines progressively stouter and longer. Inside the major (fifth) spine and behind the axis a short, blunt sixth spine. Pairs of coarse tubercles on each axial ring, median tubercle at tip of axis. On pleural regions coarse tubercles situated: a) at antero-lateral corner; b) row of three in line with fourth border spines: c) row of two on ridge running out to major border spine. Dimensions of thorax and pygidium in millimeters: length (sag.) of thorax, 7.7; width (tr.) of thorax at third segment (excluding pleural spines), 6.0; width (tr.) axis of thorax at third segment, 2.0; width pygidium at anterior margin, 11.2; length (sag.) pygidium, 3.5; width axis pygidium at first ring, 2.8.

Well preserved specimens indicate that many of the coarse ornamental tubercles had an apical opening, around which may be minute granules.

Discussion.—Comparison of the types of *Leonaspis tuberculatus* with topotype material of *L. leonhardi* (Barrande, 1846) in the Museum of Comparative Zoology indicates that there are only minor differences between the two species, suggesting that they are congeneric, as Prantl & Přibyl (1949, p. 153) state. Points of difference are that in *L. leonhardi*: a) the anterior branch of the facial suture, which in both species runs along a sutural ridge, curves inward to a lesser extent so that a wider triangular portion of fixed cheek intervenes anteriorly between it and the eye ridge; b) the occipital ring lacks the median spine; c) the fourth, not the third, thoracic segment is the most anterior to bear long pleural spines; d) the pygidium is relatively longer, and a larger area of the pleural regions, with two paired border spines, is enclosed by the ridges and major border spines.

LEONASPIS WILLIAMSI, n. sp.
Pl. 57, fig. 10–16; Pl. 58, fig. 1–4, 6,7

Holotype.—USNM, from Haragan shale, Helderberg stage, Lower Devonian, at White Mound, SE. ¼ sec. 20, T. 2 S., R. 3 E., 3¼ miles west of Nebo Store, Murray county, Oklahoma. Collected by Alwyn Williams.

Other material.—USNM, MCZ 5262, same locality and horizon, collected by W. T. Allen, J. Bridge, G. Arthur Cooper, A. R. Loeblich, Jr., and Whittington. Vines Dame, SW¼ sec. 35, T. 1 S., R. 2 E., 2 miles northwest of Dougherty, Murray county, Oklahoma, collected by J. Bridge and G. Arthur Cooper; west facing scarp, SW¼, NW¼ sec. 8, T. 1 S., R. 8 E., near Old Hunton, Coal Co., Oklahoma, collected by W. E. Ham and A. R. Loeblich, Jr.

Description.—This species is exceedingly like *L. tuberculatus*, differing mainly in that the median occipital spine is short and blunt (as in the holotype, Pl. 57, figs. 10,12,13), or scarcely developed (Pl. 58, figs. 1,2), and in having only eight segments in the thorax. *L. williamsi* is the only known odontopleurid with eight thoracic segments. The complete specimens, as well as an incomplete one with the hypostome slightly displaced, reveal certain features which may be described as follows: Eye lobe large, elevated; palpebral lobe rising vertically from fixed cheek, with shallow median depression; eye surface almost hemisphaerical, so that it faced upward as well as forward, outward and backward; facets small, arranged in diagonal lines. Posterior branch of suture runs outward just outside narrow, shallow, posterior border furrow, and curves across posterior border just inside genal angle. Free cheek with broad shallow lateral border furrow, lateral

border narrowest anteriorly, widening back to genal angle. Doublure of similar width to border, rolled under; depression with raised anterior edge, situated beneath genal angle (Pl. 58, fig. 3), is socket to receive outer parts of segments during enrollment. Row of border spines increasing in length posteriorly, thick and blunt-ended, especially laterally. Cranidium juts out in front of free cheeks (Pl. 58, fig. 1), so that there is a sharp angle in the antero-lateral margin where the suture cuts it. Both branches of the suture cross the border furrows on sutural ridges. Rostrum (Pl. 58, fig. 7) defined by connective sutures that run inward across the doublure, and hence is a wide (tr.), short (sag. & exs.) plate, widest at the anterior margin. Hypostome like that of *L. tuberculatus*.

Thorax, as in *L. tuberculatus*, has first two segments with strongly bevelled pleurae lacking the long posterior spines. The remaining six segments have long posterior pleural spines, continuous with the main pleural ridge. In front of the base of the posterior spine, and terminal to the anterior pleural band, are the same types of bifid anterior pleural spines (Pl. 58, fig. 6). Isolated specimens of the pygidium (Pl. 57, fig. 11) show the same type of bifurcating spines at the antero-lateral corner as the anterior pleural spines, and there is a further projection directed anteriorly at the inner corner—an articulating process. The doublure is narrow and rolled.

External surface smooth in the furrows, elsewhere finely granulate, on dorsal surface of cephalon, axial rings and posterior pleural bands large, bluntly rounded tubercles. Latter closely and irregularly spaced on cephalon, on axial rings two pairs conspicuous, sometimes a third, on posterior pleural bands one about mid-width, one at fulcrum, additional one in between on anterior two segments, tubercles on pygidium correspondingly placed.

Discussion.—Other trilobites in the Haragan shale include *Dicranurus hamatus*, *Miraspis* sp. ind., *Probolium* sp., *Phacops raymondi* Delo, 1935, and *Reedops deckeri* Delo, 1935. The first two of these are described below.

Genus ACIDASPIS Murchison, 1839

Pseudomonaspis R. & E. RICHTER, 1917 [objective synonym].

Type species.—By monotypy, *Acidaspis brightii* Murchison, 1839.

Pl. 58, fig. 8,12; Text-fig. 1

Acidaspis brightii ÖPIK, 1937, p. 45–46, text-fig. 11,12; PRANTL & PRIBYL, 1949, p. 140.

Discussion.—Only the cephalon of the type species seems to be known, the type locality being the Wenlock limestone, Malvern Hills, England. Pl. 58, fig. 8,12 (cf. Text-fig. 1) show specimens from the same horizon at a different locality.

Two pairs of glabellar lobes well developed, separated from median lobe by deep

---

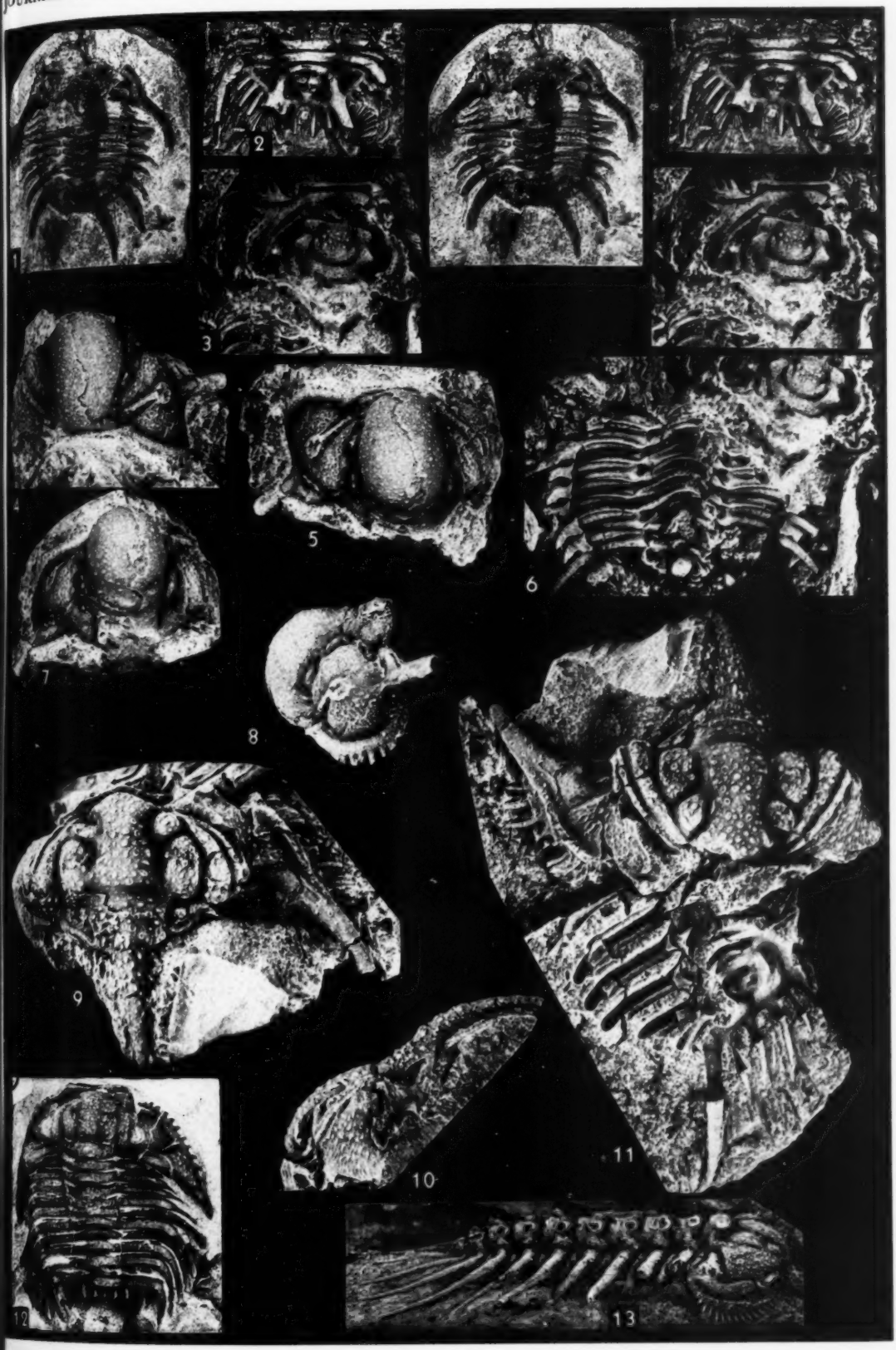
EXPLANATION OF PLATE 59

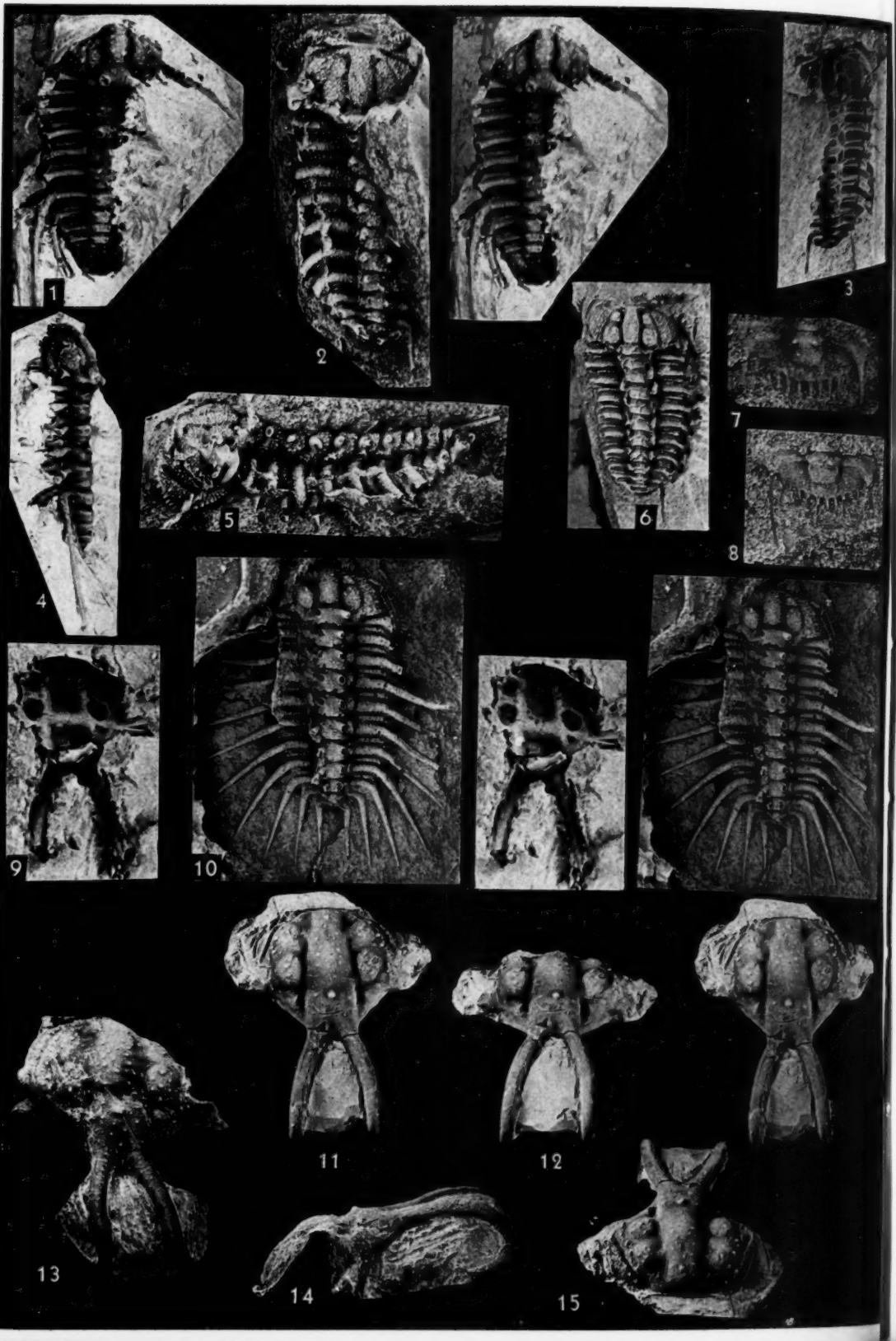
FIG. *1–3,6,9–11*—*Acidaspis cincinnatiensis* Meek. *1*, incomplete exoskeleton, dorsal stereograph, ×1.4. Maysville group, Cincinnati district, Ohio. MCZ 3688, Dyer collection. *2*, holotype, two thoracic segments and pygidium, original of Meek, 1873, pl. 14, fig. 3; dorsal stereograph, ×1.4. Fairview formation, 100 ft. below tops of hills, Cincinnati, Ohio. MCZ 4357, Dyer collection. *3,6*, incomplete disarticulated exoskeleton, exposed from ventral side, stereograph of interior of cephalon, ventral view of part of cephalon and thorax, ×4. McMillan formation?, Cincinnati, Ohio. MCZ 4359, Dyer collection. *9–11*, internal mould of cephalon combined with external mould of part of thorax and pygidium, original of Bassler, 1932, fig. 3; dorsal, left lateral, and anterior views of cephalon, ×2. Catheys limestone, upper beds, Rhodes quarry, 1½ miles southwest of Franklin, Tenn. USNM 78552.

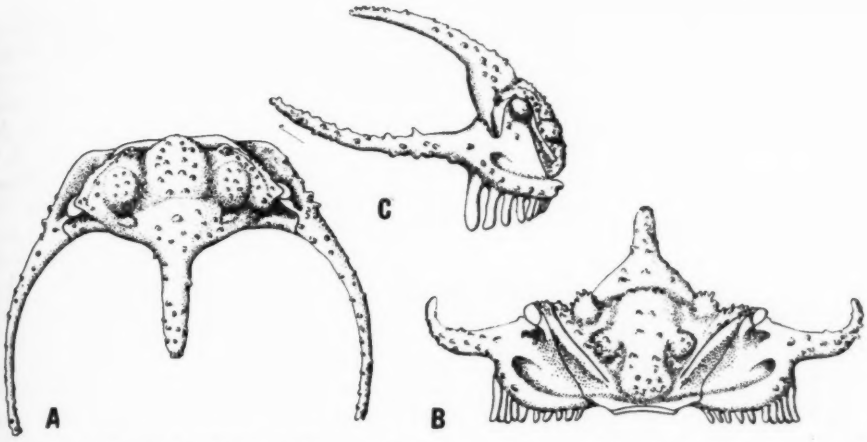
4,5,7,8—*Whittingtonia bispinosa* (M'Coy), Upper Ordovician limestone of Chair of Kildare, near Dublin, Eire. Incomplete cephalon, anterior, exterior, dorsal, left lateral views, ×3. SM A 14016a.

12—*Leonaspis coronata* (Salter), Wenlock limestone, Dudley, Worcestershire, England. Complete exoskeleton, dorsal view, ×1½. BU 679, Holcroft Collection.

13—*Proceratocephala terribilis* (Reed), Starfish bed, Upper Drummuck group, near Girvan, Ayrshire, Scotland, Latex cast of original of Reed, 1935, pl. 4, fig. 10; right lateral view, ×4. HM A 1030b.


1
2
3
4
5
6
7
8
9
10
11
12
13


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15



TEXT-FIG. *1*—*Acidaspis brightii* Murchison, Wenlock limestone, Middle Silurian, England. A, dorsal, B, anterior, C, right lateral views of cephalon. Approximately ×2. Drawn from BU 678, Pl. 58, fig. 8,12.

longitudinal furrows, in type species frontal glabellar lobe rounded, projecting well in front of anterior lateral glabellar lobes. In Ordovician species (see below) small third lateral glabellar lobes are present. Median part of occipital ring inflated and prolonged backward as median spine, separated from rest of glabella by shallow median part of occipital furrow; lateral part of occipital ring with low, gently convex occipital lobe in inner corner, behind deeper outer part of occipital furrow. Eye lobe elevated, situated opposite most posterior part of basal glabellar lobe; anterior branch of the facial suture runs straight forward and inward, diverging from the course of the eye ridge, and curves over the anterior border. The posterior branch curves downward and outward across the fixed cheek in front of the posterior border furrow, and on to the inner side of the swelling at the base of the librigenal spine, against which this furrow ends. It then curves over the posterior border, inside the base of the librigenal spine. The swelling at the base of this spine, which interrupts the posterior and lateral border furrows, is like that in *Ceratocephala* (Whittington & Evitt, 1954, p. 54, 55) and seems to be a sutural ridge. The course of the facial suture can be made out only with difficulty in *A. brightii*, and does not show on the photographs (Pl. 58, fig. 8,12). In *A. cincinnatiensis*

EXPLANATION OF PLATE 60

FIG. *1,4*—*Miraspis* sp. indet., Haragan shale, White Mound, Arbuckle Mountains, Oklahoma. Incomplete and partly crushed exoskeleton, dorsal stereograph and left lateral view, ×2. USNM.

2,3,5,6,10—*Proceratocephala terribilis* (Reed), Starfish bed, Upper Drummuck group, near Girvan, Ayrshire, Scotland. *2,5*, latex cast from original of fig. 3, dorsal and left lateral views, ×3. *3,6*, incomplete individual, counterpart moulds, original of Reed, 1914, pl. 6, fig. 7,8; ×2. BM 23147. *10*, latex cast of original of Reed, 1935, pl. 4, fig. 10; dorsal stereograph, ×3. HM A 1030b.

7,8—*Miraspis?* sp., pygidium, original of Reed, 1914, pl. 6, fig. 9. *7*, latex cast of external mould, ×2½; *8*, internal mould, ×2. Starfish bed, Upper Drummuck group, near Girvan, Ayrshire, Scotland. BM 23148.

9,11–15—*Dicranurus hamatus* (Hall), Haragan shale, Arbuckle Mountains, Oklahoma. *9*, interior of incomplete cranidium, stereograph, ×1½. White Mound. MCZ 5263. *11,12,15*, cranidium, exterior stereograph, dorsal and anterior views, ×1. Near Old Hunton. USNM. *13,14*, cranidium, exterior and left lateral views, ×2. White Mound. USNM.

it is quite clear (Pl. 58, fig. 9–11,13). Librigenal spine stout, curving backward. From the convex antero-lateral border stout spines are directed steeply downward, longest posteriorly and diminishing forward (Pl. 58, fig. 12). Anterior border, between branches of suture, projects slightly forward, and there is a notch between edge of this projection and innermost border spine.

Hypostome known in *A. cincinnatiensis* (see below). Thorax (in Ordovician species) of 10 segments, pygidium with two pairs small border spines between major pair.

Geological range.—Middle Ordovician to Middle Devonian. Species younger than Middle Silurian are rare, one example being *Acidaspis bucco* from the Middle Devonian of the Rhineland (R. & E. Richter, 1918, p. 144–145, text-fig. 1).

ACIDASPIS CINCINNATIENSIS Meek, 1873
Pl. 58, fig. 9–11,13,14; Pl. 59, fig. 1–3,6,9–11

Acidaspis anchoralis MILLER, 1875.
Acidaspis rebecca BASSLER, 1932.

Holotype.—MCZ 4357, pygidium and two thoracic segments, from 100 ft. below tops of hills, Cincinnati, Ohio. According to information kindly supplied by F. D. Holland, Jr., Curator, University of Cincinnati Museum, this implies that the specimen came from the Fairview formation (lower Maysville), and probably from the Fairmount shale and limestone member.

Other material.—The original of Plate 59, figure 1 (from the Maysville) shows that the *A. cincinnatiensis* (Meek, 1873, p. 167–169, pl. 14, fig. 3; this paper, Pl. 59, fig. 2) type of pygidium is associated with an *Acidaspis* cephalon, and excellent specimens of this cephalon, and the thorax, occur in the Corryville member, McMillan formation, upper Maysville (Pl. 58, fig. 9–11,14). *A. anchoralis* Miller (1875b, p. 349–350, fig. 23,24) came from the upper Maysville, and so this name apparently is synonymous with *A. cincinnatiensis*. The types of *A. rebecca* Bassler (1932, p. 114, fig. 3; this paper, Pl. 59, fig. 9–11) are preserved in brown, sandy limestone, and include what is probably one individual, enrolled and with thorax disjointed, and moulds of free cheeks (Pl. 58, fig. 13). Included also in the type lot is a limestone slab with a pygidium and three thoracic segments, from a different, and uncertain, locality. This material is indistinguishable from that from the Corryville, and indicates that *A. cincinnatiensis* ranges from upper Trentonian to Maysville. Additional specimens in the University of Cincinnati Museum, U. S. National Museum, and Museum of Comparative Zoology, show that a species of *Acidaspis* occurs in the Eden, though most specimens come from the Maysville, McMillan formation, and particularly the Corryville member. It seems best, until more, better localized material is available, to regard these all as one species. In this event, *A. o'nealli* Miller (1875a) is probably another synonym. The pygidium described by Anthony (1838, p. 379–380, fig. 1,2) as "*Ceratocephala ceralepta*" is, however, unrecognizable, and this name should not be used.

Description.—Cephalon differs from that of *Acidaspis brightii* in that the first and second glabellar furrows are deeper, and third glabellar lobes are distinctly outlined by their convexity and by shallow third furrows. Frontal glabellar lobe projects only slightly in front of third lateral lobes. Median part of occipital ring more elevated and backwardly extended, separated by shallow median part of occipital furrow from median glabellar lobe. Occipital spine long, length (sag.) equal to, or greater than, length (sag.) of remainder of cephalon. Both branches of the suture elevated on sutural ridges (Pl. 58, figs. 9–11), the posterior merging into inflated base of librigenal spine. The spines along the lateral border are less steeply inclined, and are distally thickened and bent postero-laterally. Hypostome (Pl. 59, fig. 3) preserved, slightly displaced, in a specimen, exposed from the ventral side, which probably came from the McMillan formation. The incomplete thorax is disjointed and displaced from the cephalon, but this displacement enabled the occipital ring and basal part of the large median spine to be exposed without having to destroy the thorax (Pl. 59, figs. 3,6). Width across shoulders of hypostome 3.25 mm., length (sag.) 2.3 mm. Middle body gently convex, subcircular in outline, middle furrow runs backward and slightly inward from ovate depression in antero-lateral corner; posterior lobe crescentic, with inflated tips.

Lateral and posterior borders of similar width; small, dorsally directed anterior wings; deep lateral notch; inflated shoulder situated at half length. Rostrum preserved in this specimen, a short (sag.), wide, plate, edge at hypostomal suture flattened, straight (except distally where it curves to meet inner edge of cheek doublure), and fits against straight, flat edge of hypostome. In this position tip of anterior wing lies immediately beneath junction of axial, preglabellar and third lateral glabellar furrows at antero-lateral corner of glabella, but no anterior boss is developed. The fit of the bevelled edges at the hypostomal suture suggests that the hypostome lies approximately in the horizontal plane, on the orientation adopted here.

Thorax of 10 segments (Pl. 59, fig. 1, in which specimen the most anterior segment is almost concealed beneath the posterior cephalic border), axis less than half width between fulcra. Pleurae divided by furrow into convex anterior band, and much more convex and wider (exs.) posterior band. Narrow (exs.) posterior flange. Posterior pleural band curves slightly backward distally, and is inflated at fulcrum, and extended into posterior pleural spine. Short, curved, blade-like anterior pleural spine (Pl. 59, fig. 6). First segment with posterior pleural spine short and bevelled to fit beneath border of cephalon. Pygidium nearly three times as wide as long. First axial ring convex, second much lower, third faint. Gently raised border to pleural regions, seven pairs border spines. Fifth are major pair, slightly upwardly directed, and connected by prominent ridge to first axial ring.

External surface finely granulate, except in deep furrows. Tubercles scattered on inflated parts of cephalon, middle body of hypostome, paired on axial rings of thorax and pygidium, two or three large tubercles on posterior pleural bands, row small tubercles on anterior band.

Discussion.—*Acidaspis* is also known from high Middle and Upper Ordovician strata in Europe, e.g., *A. viruana* Öpik (1937, p. 43–45, pl. 5, fig. 1, text-fig. 10) and *A. magnospina* Stubblefield (1928) and these species, particularly the former, are like *A. cincinnatiensis.*

Genus DUDLEYASPIS Prantl & Přibyl, 1949

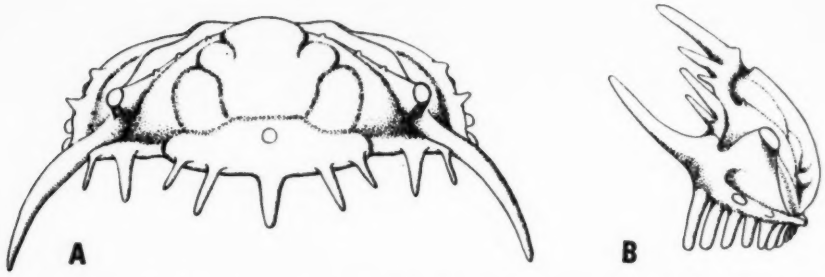
Type species.—*Acidaspis quinquespinosa* Lake, 1896

Pl. 58, fig. 5,15,16; Text-fig. 2

Lectotype (here selected).—incomplete cephalon, original of Lake, 1896, pl. 7, fig. 4, Fletcher collection, SM A 10254, from the Wenlock limestone of Dudley, Worcestershire, England.

Other Material.—B.U. 676, 677, Holcroft collection, also three additional cephala, Holcroft collection nos. 187, 220, 362, all from Wenlock limestone, Wren's Nest, Worcestershire; Holcroft collection no. 373, same horizon, Sedgley, Worcestershire.

Discussion.—The cephalon illustrated here shows the characters in more detail than did Lake's account (1896, p. 240–241, pl. 7, fig. 3,4). In front of the large basal lateral lobes the glabella narrows rapidly; there are small third lobes, third lateral furrows short, transversely directed (Pl. 58, fig. 5), frontal glabellar lobe projecting in front of third lobes. Eye lobes situated opposite mid-part of basal lateral glabellar lobes, anterior branch suture runs on sutural ridge straight forward and slightly inward to anterior border (sutural ridge appears as darker line in Pl. 58, fig. 5); suture then runs more directly inward and over outer edge of border to meet rostral suture about where anterior border projects forward (Text-fig. 2). Sutural ridge also connects eye lobe and swollen base librigenal spine, and posterior branch suture runs along inner side of ridge and over border inside base librigenal spine (Text-fig. 2). In cephalic form—particularly shape and lobation of glabella, position of eye lobe, course of suture and presence sutural ridges, presence of almost vertically-directed spines on antero-lateral border—there is a striking resemblance between *D. quinquespinosa* and *Acidaspis brightii* (compare Pl. 58, fig. 15,16, with Pl. 58, fig. 8,12). The former is distinguished from *A. brightii* and other species of *Acidaspis* by the presence of more distinct, small, third glabellar lobes, in front of which the frontal lobe projects for a relatively greater distance, the shorter, lower occipital ring, lacking lateral lobes, and smaller median occipital spine, the additional 2 pairs of spines on the posterior



TEXT-FIG. 2—*Dudleyaspis quinquespinosa* (Lake), Wenlock limestone, Middle Silurian, England. A, dorsal, B, right lateral view, approximately ×4. Drawn from BU 677, pl. 58, fig. 15,16.

border and two pairs on the occipital ring (the outer pair broken in the original of Pl. 58, fig. 15,16), the more divergent course of the anterior branches of the facial suture, and the finer tuberculate ornament. Prantl & Přibyl (1949, p. 171–172) laid stress on the different course of the anterior branch of the suture in *Dudleyaspis*, and placed it in a different subfamily from that including *Acidaspis*. I regard the similarities between *Acidaspis* and *Dudleyaspis* as indicating close relationship between the two genera, and the thorax of 10 segments, pygidium with pair of major border spines, two smaller pairs between, of *Dudleyaspis* (Lake, 1896, p. 240, pl. 7, fig. 3) also are similar to those of *Acidaspis*.

The type species has been described from the St. Clair limestone of Arkansas (Van Ingen, 1901, p. 50–51, text-fig. 12), and a similar species, *D. vanhorni* (Weller, 1907, p. 251–252, pl. 23, fig. 3,4), from the Niagaran of the Chicago area.

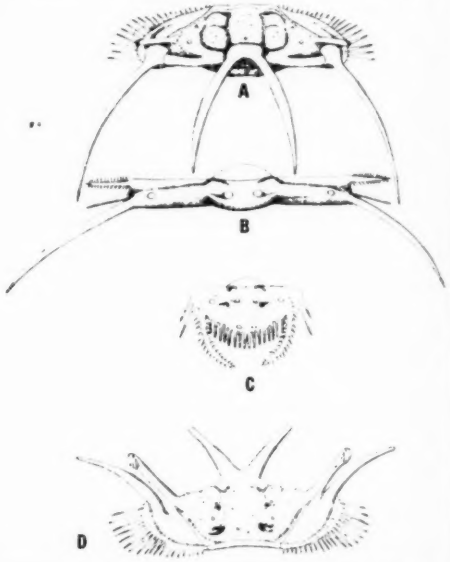
Genus MIRASPIS R. & E. Richter, 1917

Type species.—*Miraspis mira* (Barrande, 1846)

Text-fig. 3

Discussion.—Previous drawings have not made allowance for the convexity of the cephalon and the flattening that takes place in the preservation of entire specimens (such as that illustrated by Prantl & Přibyl, 1949, pl. 9, fig. 1), and so have combined an exterior view of the cephalon with a dorsal view of thorax and pygidium (Barrande, 1852, pl. 39, fig. 1). This is corrected in Text-fig. 3, and comparison with Whittington & Evitt, 1954, text-fig. 13–15, indicates the similarity between *Miraspis* and *Ceratocephala*, including the presence in both of small, low, third glabellar lobes. I regard *Miraspis* as distinguished only by relatively minor features—presence of prominent spines on antero-lateral cephalic border, eye lobe on longer stalk, thoracic pleurae ridged and bearing additional spine, different arrangement of spines on border of pygidium—and thus as a genus closely related to *Ceratocephala*. I have not seen the hypostome of *Miraspis* (Barrande, 1852, pl. 39, fig. 8,9) but it appears to be like that of *Ceratocephala* its general plan, though with distinctive features.

Only the type species, *M. mira*, has pre-



TEXT-FIG. 3—*Miraspis mira* (Barrande), Motol beds, e_{a_2}, upper Middle Silurian, Bohemia. Dorsal view of A, cephalon, B, one thoracic segment, and C, pygidium; D, anterior view of cephalon; approximately ×3. Drawn from MCZ 4195, Lištice; 4201, Lodenice.

viously been known with certainty, from the upper Wenlockian of Bohemia and Sweden, and beds of similar age in the Carnic Alps. *M. gibbosa* (Münster, 1840) may be a second Silurian species (Prantl & Přibyl, 1949, p. 196–197). A new species from the Lower Devonian of Oklahoma is described below. Reed (1935, p. 37–38, pl. 3, fig. 21) referred an incomplete cranidium from the Middle Ordovician of Scotland to this genus, but this reference is uncertain (cf. Prantl & Přibyl, 1949, p. 195). The pygidium from the Upper Ordovician of Scotland (Reed, 1914, pl. 6, fig. 9; this paper, Pl. 60, fig. 7,8) which Reed believed belonged to *Proceratocephala terribilis*, is here shown not to belong. It is of characteristic *Miraspis* type, but the associated thorax and cephalon are so far unknown.

Evidently the *Miraspis* type of pygidium is present in at least Upper Ordovician times, but the nature of the remainder of the exoskeleton being unknown, the geological range of *Miraspis* remains indefinite, though it is much greater than had been supposed.

MIRASPIS sp. indet.
Pl. 60, fig. 1,4

Material.—incomplete, crushed specimen, Lower Devonian, Haragan shale, White Mound, SE¼ sec. 20, T. 2 S., R. 3 E., 3¼ miles west of Nebo store, Murray County, Oklahoma. USNM.

Description.—The cephalon has the anterior part missing, eye lobe broken off, and the free cheeks are pushed in under the cranidium. Nevertheless, the characteristic features of *Miraspis* are shown—glabellar lobation, form of occipital ring and paired spines, row of spines on cephalic border. The eye lobe is farther forward than in *M. mira*, being opposite the first (basal) glabellar furrow, and it is not known whether the eye lobe is on a long stalk. The thorax has nine segments, prominent paired spines on axial rings, well-marked posterior ridges on pleurae which run out into the posterior pleural spines and display almost identical curvature and inclination to those of *M. mira*. The anterior pleural spine is downwardly directed, and the third pleural spine of *M. mira*, which is very slim, has not been seen. Pygidium of characteristic *Miraspis* form, five pairs of small spines between the major pair, which latter curve inward and upward. Scattered coarse tubercles on cranidium, large tubercle at fulcrum on posterior pleural ridge, pair spines on anterior ring of pygidium, and pair of tubercles on posterior border behind axis—all as in *M. mira*.

There seems no doubt as to the affinities of this specimen. The only other record of *Miraspis* in North America seems to be that of *M. whitfieldi* (Hitchcock, 1903), from a drift boulder supposedly of Marcellus shale age. These specimens considerably extend the geographical and stratigraphical range of the genus from the upper Wenlock of Europe.

Genus PROCERATOCEPHALA Prantl & Přibyl, 1949

Drummuckaspis PRANTL & PŘIBYL, 1949 [subjective synonym].

Type species.—*Acidaspis terribilis* Reed, 1914
Pl. 59, fig. 13; Pl. 60, fig. 2,3,5,6,10

Lectotype (here selected).—B.M. In 23147, counterpart moulds, original of Reed, 1914, pl. 6, fig. 7,8, this paper, Pl. 60 fig. 3,6, from Upper Ordovician, Starfish Bed, Upper Drummuck Group, Thraive Glen, Girvan, Scotland.

Other material.—HM A 1030 a,b, counterpart moulds, originals of Reed, 1935, pl. 1, fig. 22, pl. 4, fig. 10; HM A 3992, internal mould; all same locality and horizon. HM A 1030 a,b, were described by Reed (1935, p. 38–39) as a new species "*Acidaspis* (*Ceratocephala*) *discreta*," later made the type of *Drummuckaspis* Prantl and Přibyl, 1949, p. 202–204.

Discussion.—The latex casts from the two external moulds mentioned above (Pl. 60, fig. 2,5,10) suggest to me that there is no reason for thinking that these specimens represent different species, let alone distinct genera. Reed (1914, pl. 6, fig. 9,10; this paper, Pl. 60, fig. 7,8) associated an isolated pygidium with the lectotype of *P. terribilis*, but the external mould of the latter clearly shows a quite different pygidium, with a median spine and one pair of backwardly directed border spines (the three pits may be seen in Pl. 60, fig. 3, but unfortunately

the latex did not penetrate these pits in making the cast, Pl. 60, fig. 2,5). The paired spines, and a faint median spine, are preserved in the second specimen (Pl. 60, fig. 10), and HM A 3992 also shows the short median spine.

It appears to me that in both specimens the highly convex cephalon has been crushed during compaction of the sediments and that breaks run across the cheeks roughly along the line of the suture. Therefore, we do not see the complete cheeks, and the position and size of the eye lobe, form of free cheek and border, are uncertain. The lectotype shows the glabella (Pl. 60, fig. 2) with a tiny third pair of lateral lobes fused with the fronto-median lobe, the deep furrow defining the median lobe, the deep occipital furrow and the anterior part of the fixed cheeks and eye ridges. Outside the break, on the left side (Pl. 60, fig. 5), the broad lateral border and border furrow of the free cheek, and base of the librigenal spine, are preserved. In the original of Pl. 59, fig. 13, and Pl. 60, fig. 10, the occipital ring, posterior border and deep, broad border furrow, and broad (tr.) convex right fixed cheek are preserved, but outside this only what appear to be broken strips of the free cheek. The position of the eye lobe may be indicated by the projection just inside the break, situated far forward and outward, in line with the second glabellar lobe.

The paired spines of the occipital ring and axial rings were stout, curving upward and outward, and situated on the anterior portion of each ring. Antero-lateral corner of each ring inflated. Pleurae divided by deep furrow into a narrow (exs.) anterior and a broad (exs.) posterior convex band. From the termination of the anterior band a short, blade-like spine with barbs projected downward (Pl. 60, fig. 5), while the spines of the posterior band are shown in Pl. 60, fig. 10. Nine thoracic segments. Pygidium short (sag.), with one prominent axial ring connected by ridges to the pair of major border spines.

The likeness between *Proceratocephala terribilis* and recently described species of *Ceratocephala* (Whittington & Evitt, 1954) is considerable, the main distinctions between them being that in *P. terribilis:* 1) the median glabellar lobe is relatively narrower and defined by deeper furrows laterally and the deeper occipital furrow; 2) the paired axial thoracic spines are far longer and stouter, the antero-lateral parts of the axial rings more inflated, and the pleurae are ridged and furrowed; 3) the pygidium is apparently relatively smaller in size, but the paired major spines are stouter. These distinctions are applicable also as between *P. terribilis* and the type and other Silurian species of *Ceratocephala*, some of which have 10 thoracic segments and a greater number of border spines on the pygidium.

As Prantl & Přibyl (1949, p. 193) pointed out, there are some characters in common between *P. terribilis* and the upper Wenlockian *Miraspis mira* (Text-fig. 3)—the deep furrows bounding the parallel-sided median glabellar lobe, the form of the axial rings and ridged pleurae, and the number of thoracic segments. However, the eye lobes in *Proceratocephala* cannot be in the same position as in *Miraspis*, the paired occipital spines are slimmer, and the pygidia of the two species are different, that of *M. mira* being relatively larger, the border with one pair of stout spines and many pairs of small spines.

I have here regarded both *Proceratocephala* and *Miraspis* as distinct genera. They are clearly closely related to *Ceratocephala*, and perhaps independently derived from it.

Genus WHITTINGTONIA Prantl & Přibyl, 1949

Type species.—Acidaspis bispinosus M'Coy, 1846.

Pl. 59, fig. 4,5,7,8

Discussion.—The type and only known species was first described by M'Coy (1846, p. 45, pl. 4, fig. 7), and later by Salter (1853, pl. 6, p. 4–8, fig. 4–6), and came from the Upper Ordovician limestone at the Chair of Kildare, Eire. Later Warburg (1925, p. 248–252, pl. 6, fig. 2,3) described specimens from the Upper Ordovician Boda (upper Leptaena) limestone, Sweden; Prantl & Přibyl (1949, p. 205–207, pl. 5, fig. 7) made this species the type of a new genus, and Erben (1952) considers that it is probably related to *Ceratocephala*. I have not seen the holotype, nor the specimen described by Salter, but have examined topotype material

in the Palaeontological Institute of Uppsala and the Sedgwick Museum, Cambridge. All of these specimens are parts of cephala, and many are compressed and distorted, but the one incomplete cephalon illustrated here appears to be preserved without much distortion. Though Warburg gave a detailed description, her illustrations are unsatisfactory, and the use of Salter's drawing by Prantl & Přibyl, and by Erben, does not convey an accurate impression of the characters. The occipital ring bears prominent paired spines curving upward and outward, a low median tubercle, faint occipital lobes, and lacks the posterior band. Only the outermost part of the occipital furrow, behind the basal lateral lobe, is deep. Frontomedian glabellar lobe occupying most of width between axial furrows, strongly convex lateral slopes almost vertical, and overhanging the anterior border; narrow, gently convex band across base; three pairs of narrow (tr.) gently convex lateral lobes, the anterior pair small, subcircular in outline. Shallow preglabellar furrow, and narrow (sag. and ex.) anterior border running transversely in front of glabella, outside projected line of axial furrow curving back, then curving outward again to merge with cheek border. Cheek convex, sloping steeply antero-laterally and extended so that margin forms almost a semi-circular curve; broad convex border, row of short, blunt spines on lateral margin directed outward and downward. Eye lobe about central on cheek, prominent eye ridge runs inward and forward to merge with frontal glabellar lobe in front of third lateral lobe. Anterior branch of suture runs forward and inward on low sutural ridge in straight line to cross anterior border at inner edge of notch; course diverges at slight angle from that of eye ridge (Pl. 59, fig. 4,5). Posterior branch also on sutural ridge, and runs back from eye lobe almost in line with anterior branch until it curves in "S" over posterior border just within base of librigenal spine (Pl. 59, figs. 7,8). Latter curves upward as well as postero-laterally and base merges with borders and sutural ridge. Posterior border ends at inner end against ridge formed by merging of inner corner of fixed cheek and anterolateral part of occipital ring. External surface granulate, with scattered larger tubercles which are largest and densest on glabella and inner part of cheeks.

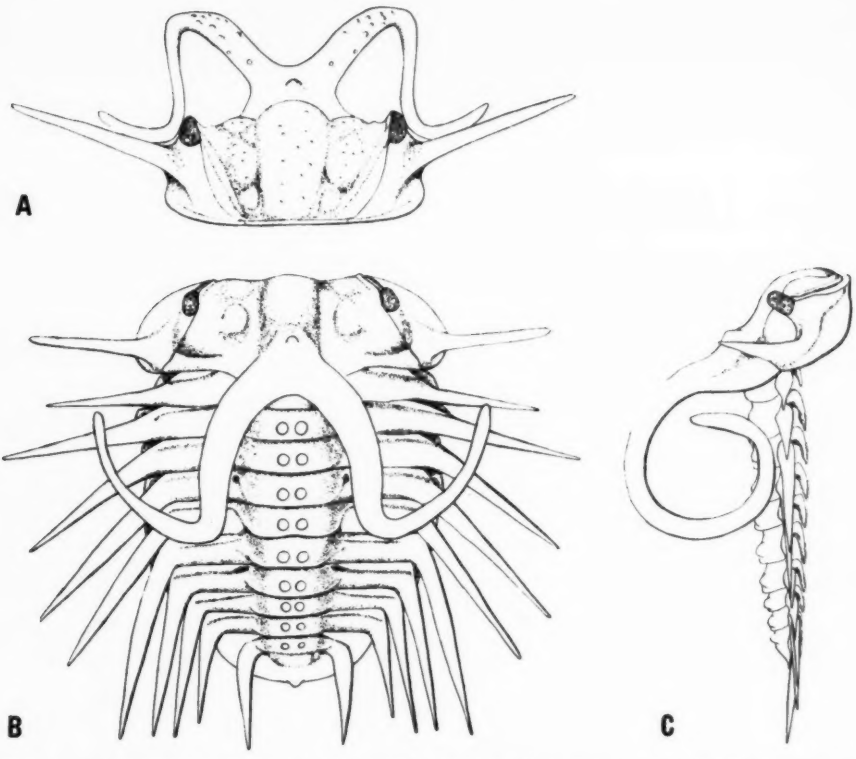
The trapezoidal cephalic outline, transverse convexity, number of lateral glabellar lobes, shape of cheeks, presence of eye and sutural ridges, etc., of *Whittingtonia* are like those of *Ceratocephala*, and I regard it as a closely related genus, probably derived from *Ceratocephala*. The relative width and convexity of the fronto-median glabellar lobe, and the different position of the eye lobe, distinguish it at once. Both branches of the facial suture can be traced in *Whittingtonia*, and I do not think that the free and fixed cheeks were necessarily partly fused (as claimed by Prantl & Přibyl, 1949, p. 206), nor that this condition would be of generic significance if it occurred (cf. Whittington & Evitt, 1954, p. 53).

Genus DICRANURUS Conrad, 1841

Type species.—Acidaspis hamata Hall, 1859.

Discussion.—Conrad (1841, p. 48) proposed the name *Dicranurus* without a nominal species, giving a description and locality. On another page of the same report Conrad (1841, p. 25) listed *Dicranurus hamatus*. Not until Hall (1859, p. 371; 1861, pl. 79, fig. 15–19) published his description and figures, listing Conrad's names in the synonymy, did the species *D. hamatus* have validity. Conrad did have figures prepared to accompany his report of 1841, but these figures do not accompany most copies of the report (Vogdes, 1890, p. 33;1893, p. 39). Conrad's figure of *Dicranurus hamatus* was reprinted both by Hall (1862, pl. 11, fig. 1) and by Clarke (1892, pl. 1, fig. 5).

The four or five species placed in this genus are similar, and judging from published figures the material of *Dicranurus monstrosus* (Barrande, 1852) in the Museum of Comparative Zoology is among the most complete in existence. The restorations (Text-fig. 4) are based on these specimens, and show the cephalon in what is believed to be the correct position. Three pairs of glabellar lobes are present, the third small and depressed, as in *Ceratocephala* or *Miraspis*. The longitudinal furrows bounding the median glabellar lobe are continuous with the longitudinal furrows which divide the occipital ring into a raised central por-



TEXT-FIG. 4—*Dicranurus monstrosus* (Barrande), Prokop limestones, g_{α_2}, Middle Devonian, Lochkov, Bohemia. A, anterior view of cephalon, B, C, dorsal and right lateral views of entire exoskeleton, approximately ×1½. Drawn from MCZ 4377, 4378, 4381, 4382.

tion (swollen base of the paired spines) and lower lateral portions. Anterior pleural spines have been described as "short, stunted" (Prantl & Přibyl, 1949, p. 187) but in *D. monstrosus* they are directed downward and outward, proximally slightly forward, but distally curving back and becoming blade-like in form, with lateral barbs. The curved occipital spines are preserved in three specimens in the Museum of Comparative Zoology, and the form is essentially the same as that of the specimen illustrated by R. & E. Richter (1930, text-fig. 6), which comes from the same locality.

Raymond (1916, p. 138) commented on the presence in *Dicranurus* of two main spines on the pygidium, and the lack of the usual border spines, and compared this pygidium with that of *Selenopeltis*. He might have also compared the thoracic segments, which in *Dicranurus* have faint lateral axial lobes and gently forward-curving pleural ridges, while in *Selenopeltis* the same features are strongly developed. Both genera also lack spines on the anterolateral cephalic border. This seems to me to demonstrate the homogeneity of odontopleurid characters, and their repetition in time. I regard the cephalon of *Dicranurus* as being closest, however, to that of *Ceratocephala* and *Miraspis* (in form, glabellar lobation, position of eye lobes, nature of librigenal and occipital spines, etc.).

Dicranurus is known from the Lower and Middle Devonian of North America, Bohemia, and Australia.

DICRANURUS HAMATUS (Hall, 1859)
Pl. 60, fig. 9,11–15

Material.—Cranidium from Lower Devonian, Haragan shale, west facing scrap, SW¼ of NW¼, Sec. 8, T. 1 S., R. 8 E., near Old Hunton, Coal Co., Oklahoma; USNM. Incomplete cranidium exposed from inner

side (MCZ 5263), incomplete cranidium (USNM), Haragan shale, White Mound, SE¼ Sec. 20, T. 2 S., R. 3 E., 3¼ miles west of Nebo store, Murray county, Oklahoma. Collected by G. Arthur Cooper, W. E. Ham, A. R. Loeblich, Jr., and Whittington.

Description.—Comparison shows the close similarity between the Oklahoma specimens and those from New York, though the Oklahoma cranidium is unusually well preserved and has the outer surface of the exoskeleton. The glabella is divided by broad, deep furrows into a median (fronto-median glabellar lobe and median part of occipital ring, separated by shallow occipital furrow) portion which stands highest, and lateral portions. The latter includes the 3 lateral glabellar lobes (the anterior low and faint, defined by a very shallow glabellar furrow) and the outer part of the occipital ring, which is inflated at the inner corner, adjacent to the occipital furrow. This inflation is somewhat greater than that in *D. monstrosus*. The occipital spines appear to be complete, the distal curve modified somewhat by crushing, the tips blunt. The New York specimens have the same type of spines, which contrast with the longer, more curved occipital spines of *D. monstrosus* (Text-fig. 4). Palpebral lobe steeply sloping, with low rim which merges anteriorly into the gently convex eye ridge (Pl. 60, fig. 13). External surface smooth in the furrows, finely granulate elsewhere, with scattered large tubercles not symmetrically arranged. Largest such tubercle is the median occipital.

REFERENCES

ANTHONY, J. G., 1838, *Ceratocephala ceralepta:* Am. Jour. Sci., vol. 34, p. 379–380, 2 fig.

BARRANDE, J., 1852, Système Silurien du centre de la Bohême; vol. I, Prague and Paris.

BASSLER, R. S., 1932, The stratigraphy of the Central Basin of Tennessee: Tennessee Div. Geol., Bull. 38, p. x+1–268, pl. 1–49, maps.

CASTELNAU, F. DE, 1843, Essai sur le Système Silurien de l'Amérique septentrionale: Paris, p. 1–56, 24 pl.

CLARKE, J. M., 1892, Notes on the genus *Acidaspis:* N. Y. State Mus., 44th Ann. Rept., p. 91–101, pl. 1–3.

——, & RUEDEMANN, R., 1903, Catalogue of type specimens of Paleozoic fossils in New York State Museum: N. Y. State Mus., Bull. 65, p. 1–847.

CONRAD, T. A., 1840, Third Annual Report, Palaeontological Department, Geological Survey of New York, Albany: Assembly no. 50, p. 199–207.

——, 1841, Fifth Annual Report, Palaeontology of the State of New York, Albany, Assembly no. 150, p. 25–57.

DELO, D. M., 1935, New Phacopinae from the Devonian of Oklahoma and Iowa; Jour. Paleont., vol. 9, p. 421–423, pl. 48.

ERBEN, H. K., 1952, Zur Gliederung der Ceratocephalidae Rud. & E. Richter, 1925, emend. Prantl & Přibyl, 1949 (Tril.): Neues Jahrbuch, vol. 7, p. 304–317. 3 fig.

HALL, J., 1859–1861, Geological Survey of New York, Palaeontology: vol. 3, Albany, p. 1–532 (1859), pl. 1–120 (1861).

——, 1862, Contribution to Palaeontology: 15th Ann. Rept., New York State Cabinet Nat. Hist., p. 1–198, pl. 1–11. (p. 1–112 published in advance, 1861).

HITCHCOCK, C. H., Notice of a species of *Acidaspis* from a boulder of Marcellus shale, found in drift, at West Bloomfield, New Jersey: Am. Mus. Nat. Hist., Bull., vol. 19, p. 97–98, pl. 6.

LAKE, P., 1896, The British Silurian species of *Acidaspis:* Geol. Soc. London, Quart. Jour., vol. 52, p. 235–245, pl. 7, 8.

M'COY, 1846, A synopsis of the Silurian fossils of Ireland: Dublin, p. 1–72, pl. 1–5.

MEEK, F. B., 1873, Descriptions of invertebrate fossils of the Silurian and Devonian systems: Rept. Geol. Surv. Ohio, vol. I, part 2, p .1–243, pl. 1–23.

MILLER, S. A., 1875a, *Acidaspis o'nealli*—(S. A. Miller): Cincinnati Quart. Jour. Sci., vol. 2, p. 86–87, fig. 9.

——, 1875b, Some new species of fossils from the Cincinnati group and remarks upon some described forms: Cincinnati Quart. Jour. Sci., vol. 2, p. 349–355, fig. 23–26.

ÖPIK, A., 1937, Trilobiten aus Estland: Pub. Geol. Inst. Univ. Tartu, no. 52, p. 1–163, pl. 1–27.

PRANTL, F., & PŘIBYL, A., 1949, A study of the superfamily Odontopleuracea nov. superfam. (Trilobites); Rozpravy, sv. 12, Stát. Geol. Úst. Československé Rep., Praha, p. 1–221 (Czech & English texts, Russian summary), pl. 1–11, text-fig. 1.

RAYMOND, P. E., 1916, The genera of the Odontopleuridae: Ottawa Naturalist, vol. 29, p. 135–139.

REED, F. R. C., 1914, The Lower Palaeozoic Trilobites of Girvan, Supplement: Palaeontographical Soc., London, p. 1–56, pl. 1–8.

——, 1935, The Lower Palaeozoic Trilobites of Girvan, Supplement. 3: Palaeontographical Soc., London, p. 1–64, pl. 1–4.

RICHTER, R., 1932, Crustacea *in* Handwörterbuch der Naturwissenschaften, 2nd Ed., Jena, vol. 2, p. 840–864, fig. A, 1–65.

——, & RICHTER, E., 1917, Über die einteilung der familie Acidaspidae und über einige ihrer devonischen vertreter: Centralbl. f. Min., Jahr 1917, p. 462–472.

——, & ——, 1918 Paläontologische beobachtungen im Rheinischen Devon. I: Jahrb.

Nassauischen Ver. Nat., Wiesbaden, Jahr. 70, p. 143–161, pl. 1.

——, & ——, 1930, Neue Hörner—Trilobiten in unserer Schausammlung: Natur und Mus., vol. 60, p. 31–45, 10 fig.

——, & ——, 1952, Die Typen von *Proetus tenuimargo* und *Leonaspis aries:* Senckenbergiana, vol. 33, p. 109–113, pl. 4, fig. 25–27.

RUEDEMANN, R., 1930, Geology of the Capital District: N. Y. State Mus. Bull., no. 285, p. 1–218, 79 fig., map.

SALTER, J. W., 1853, Figures and descriptions illustrative of British organic remains: dec. 7, pl. 6, Mem. Geol. Surv. U.K., p. 1–7.

STUBBLEFIELD, C. J., 1928, A new trilobite, *Acidaspis* (*Pseudomonaspis*) *magnospina*, from the Coniston limestone: Ann. Mag. Nat. Hist., London, ser. 10, vol. 1, p. 427–433, pl. 14.

VAN INGEN, G., 1901, The Silurian fauna near Batesville, Arkansas. Pt. II, Paleontology: Trilobita: School Mines Quart., Columbia U., vol. 23, p. 34–74, fig. 3–22.

VOGDES, A. W., 1890, A bibliography of Paleozoic Crustacea from 1698 to 1889: U. S. Geol. Surv., Bull. 63, p. 1–177.

——, 1893, A classed and annotated bibliography of the Palaeozoic Crustacea: Occ. Papers California Acad. Sci., p. 1–412.

WARBURG, E., 1925, The trilobites of the Leptaena limestone in Dalarne: Geol. Inst. Uppsala, Bull., vol. 17, p. 1–446, pl. 1–11, fig. 1–22.

WELLER, S., 1907, The paleontology of the Niagaran limestone in the Chicago area: Chicago Acad. Sci., Bull. 4, pt. 2, p. 163–281, pl. 16–25.

WHITTINGTON, H. B., 1950, A monograph of the British trilobites of the family Harpidae: Palaeontographical Soc., London, p. 1–55, pl. 1–7, 16 fig.

——, 1953, North American Bathyuridae and Leiostegiidae (Trilobita): Jour. Paleont., vol. 27, p. 647–678, pl. 65–69, 5 fig.

——, & EVITT, W. R., 1954, Silicified Middle Ordovician trilobites: Geol. Soc. Am., Mem. 59, p. 1–137, pl. 1–33, 27 fig.

MANUSCRIPT RECEIVED JUNE 10, 1955.

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 521–530, PL. 61, 1 TEXT-FIG., MAY 1956

NEW PENNSYLVANIAN BRACHIOPODS

G. ARTHUR COOPER
U. S. National Museum, Washington, D. C.

ABSTRACT—Four new species are described, three belonging to new genera, and the fourth, to a genus (*Stensocisma*) not before identified from Pennsylvanian rocks of the United States. *Psilocamara* is a new name for a group of stenoscismatid species improperly described as *Levicamera*. Another new genus, *Cardiarina*, introduces structures not before seen in American brachiopods, and *Oligothyrina* is an unusual terebratuloid. The new species are *Pilocamara renfroarum*, *Oligothyrina alleni*, *Cardiarina cordata*, and *Stenoscisma bowsheri*.

INTRODUCTION

THREE of the species described in this paper were taken from silicious residues resulting from the solution of limestone taken from the upper part of the Magdalena formation in upper Grapevine Canyon, Sacramento Mountains, New Mexico. The fossiliferous ledge, about 50 feet below the Abo sandstone, is about 9 to 12 inches thick, composed of smooth, impure limestone. The residues produced many of the common Pennsylvanian genera in abundance in addition to the species described herein. The most abundant macroscopic brachiopod is a terebratuloid resembling *Cryptacanthia* which was the chief objective in making the collection.

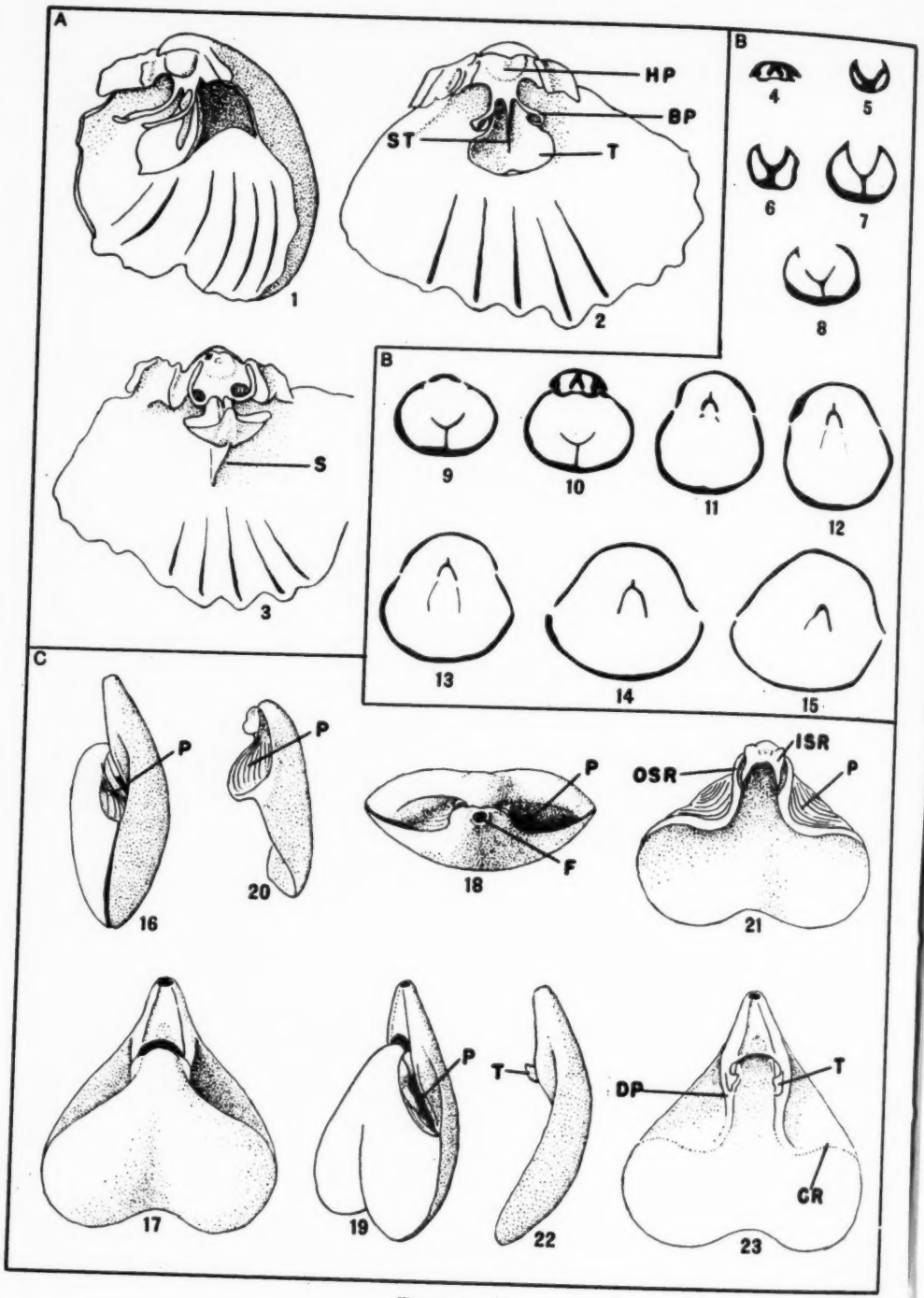
The silicious residues produced many immature and small brachiopods, among them two species here referred to new genera. Most of the small specimens proved to be young of larger species and included *Cleiothyridina*, *Punctospirifer*, *Dielasma*, *Kozlowskia* and *Stenoscisma*. *Composita*, which is usually abundant in Pennsylvanian faunas is rare in this one. Many of the immature specimens are sufficiently well-preserved to provide important information on the development of interior structures of several genera.

Of much interest in the silicious residues is the occurrence of *Stenoscisma*, a genus hitherto not described or reported from the Pennsylvanian. It is fairly common in this upper Magdalena horizon. In this connection specimens of *Psilocamara* from north central Texas are also of interest. In describing both these genera need arose for a term to characterize the brachial muscle supports of these two genera and the Stenoscismatacea in general.

Before now the term cruralium was used to define the spoonlike muscle platform of the Stenoscismatacea. This name however is inappropriate because the cruralium of the Stenoscismatacea is not constructed like that of the Pentameracea or like that of rhynchonellids such as *Camarotœchia* to which the name has been commonly applied.

The typical cruralium is formed by the union of crural plates (supporting plates) uniting with a median septum to form a chamber under the beak. The term cruralium discretum is used when the crural plates attach to the valve floor.

It is proposed to call the brachial plate in the Stenoscismatacea the torynidium from the Greek *toryne*, a spoon. In most genera it is a shallow spoon-shaped plate supported wholly or in part by a thin median septum, duplex in character. The floor of the spoon may be occupied by a low median septum. The spoon is often trilobate at its free end, the median lobe protruding anterior to the end of the median septum. The torynidium and hinge-plate appear to be completely separate. The attached end of the torynidium extends under the crura and their attachments. The crural bases and crura overhang the spoon-shaped plate. It is thus evident that the torynidium is not formed by coalescence of crural supporting plates with septum. In many specimens the hinge-plate and torynidium are welded by callus deposit. Furthermore, the small septum inside the spoon may attach to the hinge-plate (see Weller, 1914, p. 169, fig. 1e; Belanski, 1928, p. 24, fig. 11e). This is a



TEXT-FIG. *1*

Drawings in A and C by Lawrence B. Isham

A. *Stenoscisma venustum* (Girty)

1–3—Respectively side, posterior and anterior views of the brachial interior showing the torynidium

common condition in this superfamily, but *Psilocamara* described herein is not provided with this small septum.

Illustrations of the torynidium of *Stenoscisma venustum* (Girty) from the Glass Mountains of west Texas are introduced (Text-fig 1A, no. 1–3) to show the form of this structure.

SYSTEMATIC DESCRIPTIONS

Genus PSILOCAMARA n. gen.

Levicamera GRABAU, 1934, Palaeont. Sinica, ser. B, vol. 8, fasc. 3, p. 18.
Laevicamera GRABAU, 1936, ibid., fasc. 4, p. 87.

Biconvex, with the brachial valve having the greater depth; outline subpentagonal; anterior commissure uniplicate, pedicle tongue usually angular. Surface marked only by concentric lines of growth. Pedicle valve with strongly incurved beak and well-developed spondylium. Brachial valve having a torynidium.

Type species.—*Psilocamara renfroarum* n. sp.

Discussion.—This genus differs from *Stenoscisma* and *Nantanella* in having a smooth, non-plicated exterior; otherwise it is similar to other members of the Stenoscismatidae. It comprises the same group of shells referred to *Levicamera* by Grabau, but Grabau failed to define his genus when it was first proposed and also failed to make an "unambiguous designation" of a type species.

The name *Levicamera* was first proposed in 1934 when Grabau described the species *L. athyriformis*. The genus was not characterized at that time, but in a footnote (Grabau, 1934, p. 18) Grabau stated that the genus would be characterized in a forthcoming publication (Palaeont. Sinica, ser. B, vol. 7, fasc. 4). In the same footnote "*L. yunnanensis* Grabau, n. sp." is designated as the type species of the genus. This designated type was undescribed at the time. Consequently, the genus *Levicamera* at this time had no availability or validity because of failure to characterize the genus and failure to designate a valid type species.

Two years later Grabau (1936, p. 87–90) used the name *Laevicamera* again but with a slight variation in the spelling. In this instance two described species *Camerophoria sella* Kutorga and *C. pentameroides* Tschernyschew are referred to the genus and another new species *L. ? martiniodes* is described. In this publication Grabau characterizes the genus as comprising "smooth Camerophoridae, usually with a tuning fork type of spondylium." This statement makes it clear what Grabau means by *Laevicamera*, but again in this publication a footnote (p. 87) gives reference to another future publication (Palaeont. Sinica, ser. B, vol. 9, fasc. 4) in which a full generic description will be given. The genotype again is cited as *L. yunnanensis*, but it is still an undescribed species. This species is

---

in different poses, ×2. Bp = brachial process; HP = hinge-plate; S = septum; St = septum in torynidium; T = torynidium.

Permian (upper Leonard formation), ½ mile east of Split Tank Glass Mountains, Texas (ref.: 15-minute Hess Canyon Quadrangle).

B. *Psilocamara renfroarum*, n. sp.

4-15—4, Section across the beak of the brachial valve showing torynidium independent of the hinge-plate and no septum in the torynidium, ca. ×4.5, paratype USNM 124412g; *5–15*, serial sections of a complete individual showing torynidium and spondylium, ca. ×4. Distance from beak in mm.: 5 = 0.1; 6 = 0.2; 7 = 0.3; 8 = 0.45; 9 = 0.65; 10 = 0.77 (note independence of hinge-plate and torynidium); 11 = 1.0; 12 = 1.1; 13 = 1.2; 14 = 1.7; 15 = 1.9; all structures disappear after 1.21 mm.

Horizon and locality—see description.

C. *Cardiarina cordata*, n. sp.

16-23—16–19, Respectively side, brachial, posterior, and tilted views of a complete specimen showing parathyridium, foramen, and flat deltidial plate, ×20, paratype USNM 124411e; *20,21*, side and interior views of the brachial valve showing parathyridium and cardinalia, ×20, holotype USNM 124411a; *22, 23*, side and interior views of the pedicle valve, ×20, showing teeth, long dental plates and curving ridges at the anterior ends of the dental plates, counterpart to preceding brachial valve.

Horizon and locality—see description.

still undescribed and unavailable as a type. Consequently *Laevicamara* has no validity or availability.

Described species referable to *Psilocamara* are: *Camerophoria sella* Kutorga, *C. pentameroides* Tschernyschew. Grabau's *L.? martinioides* appears not to belong with the Stenoscismatidae.

PSILOCAMARA RENFROARUM n. sp.
Pl. 61,B fig. 20–32, Text-fig 1B, no. 4–15

Shell small, subpentagonal in outline, with the length and width nearly equal; valves unequal in depth, the brachial valve having the greater depth. Maximum width at about the middle. Sides narrowly rounded, anterior margin subnasute. Anterior commissure strongly uniplicate. Surface smooth.

Pedicle valve unevenly convex in lateral profile, the convexity gentle but greatest just anterior to the umbo; anterior profile faintly convex. Beak narrow, strongly incurved. Umbo gently inflated. Sulcus originating at about the middle, broad and shallow; tongue long and acutely pointed.

Brachial valve gently and fairly evenly convex in lateral profile; anterior profile narrowly arched to subcarinate. Umbo and median region swollen; fold indistinct; flanks gently swollen, with precipitous slopes.

Interior.—Some details of the interior are visible through the yellow translucent shell, especially the length of the septa buttressing the spondylium and the torynidium. The total length of the spondylium as seen on the exterior of the holotype is 3.25 mm. The spondylium is sessile in the posterior part. The spondylium of the figured paratype is 2.5 mm. long, but the spondylium chamber is about 1.5 mm. of this length. In the brachial valve the torynidium and septum in each of the specimens cited above is about 1 mm. long. This structure has about the same dimension in all of the measured paratypes. The torynidium is also sessile at the rear but becomes considerably elevated above the valve floor in the interior.

Serial sections give additional details of the interior. The spondylium is shorter than the torynidium and disappears about one millimeter anterior to the beak. In studying the sections it should be borne in mind that the pedicle valve is strongly umbonate. Therefore, sections cut parallel to a tangent to the umbo will exaggerate the length of the septum. The spondylium in this species actually rests on a low septum not a high one as the exaggerated sections suggest.

In the brachial valve the median septum of the torynidium is short but continues along the base of the spoon-like plate for nearly its full length. In studying the sections of this valve it must also be borne in mind that the sections are strongly oblique to the structures which are thus exaggerated. No median septum buttresses the hinge-plate (section 10) in this species as it does in many species of *Stenoscisma*. Not enough interiors of *Psilocamara* are known to indicate the importance of this lack of a septum.

Measurements in mm.—	length	brachial length	width	thickness
Holotype 124412a	7.4	6.5	6.9	5.1
Paratype 124412b	6.8	5.8	6.5	4.8
Paratype 124412c	6.5	5.5	5.5	4.6
Paratype 124412d	6.5	5.6	5.4	4.5
Paratype 124412e	6.3	5.4	5.5	4.2
Paratype 124412f	5.4	4.9	4.8	4.0
Figured specimen 124415	4.9	4.3	4.3	3.5

Types.—Holotype USNM 124412a; figured paratype 124412b; unfigured paratypes: USNM 124412 c-f; figured specimen USNM 124415.

Horizon and locality.—Pennsylvanian (Capps formation), road cut on Texas Highway 148, 5.7 miles north of its junction with Texas Highway 199, north-northwest of Jacksboro, Jack County, Texas.

Pennsylvanian (Henrietta formation, Fort Scott member, Cycle C, member 7), Pershing Avenue and Cleveland Walk, University City, St. Louis County, Mo. (Knight locality 42).

Pennsylvanian (Cherokee formation, *Chaetetes* limestone), 0.6 mile west of Lackland Station on the C., R. I., and P. RR., one mile northwest of Stratman, St. Louis County, Mo. (Knight locality 43).

Discussion.—This species is characterized by its stenoscimatoid interior, smooth ex-

terior with angular tongue on the pedicle valve. No other American species of this genus is known to which the present one may be compared, but the genus is known in the Permian of Europe and Asia. *Psilocamara sella* (Kutorga) is similar to the American species but is much larger and has a deeper sulcus, more triangular outline and wider anterior region.

STENOSCISMA BOWSHERI, n. sp.
Pl. 61,D, fig. 42–55

Small, wider than long, subpentagonal in outline; greatest width at the middle; sides narrowly rounded; anterior margin nearly straight. Anterior commissure strongly uniplicate. Surface smooth except for the fold and sulcus which are occupied by three and two costae respectively.

Pedicle valve gently convex in lateral profile and with the maximum convexity just posterior to the middle; anterior profile broadly and gently convex. Beak small, incurved. Umbo narrowly rounded, and median region gently inflated. Flanks moderately steep. Sulcus originating just anterior to the middle, shallow and bounded on each side by a short oblique and angular fold. Tongue long and truncated anteriorly.

Foramen triangular, open, no deltidial plates having been seen in any of the specimens studied.

Brachial valve deeper than the pedicle valve but with a gently convex lateral profile; anterior profile strongly arched. Fold low, originating at about the middle; flanks gently swollen and precipitous.

Pedicle valve interior with a shallow and short spondylium; interior of brachial valve having a strongly elevated but shallow torynidium anteriorly trilobed, the median lobe projecting noticeably beyond the lateral ones.

Measurements in mm.—	length	brachial length	width	thickness
Holotype 124408a	8.4	7.4	9.7	6.1
Paratype 124408b	7.8	7.0	9.2	4.8
Paratype 124408c	8.0	7.0	9.2	5.8
Paratype 124408d	7.9	7.9	8.5	6.4
Paratype 124408e	7.5	6.7	7.1	5.4

Types.—Holotype USNM 124408a; figured paratypes: USNM 124408b, 124408g,h,i; unfigured paratypes: USNM 124408c-f, j-m.

Horizon and locality.—Magdalena formation (30–40 feet below top), ½ mile south of Old Juniper, from a small draw which crosses the road center E½, SW¼ sec. 25, T. 19 S., R. 11 E., upper Grapevine Canyon, Sacramento Mountains, Otero County, New Mexico. Forest Service Map of Lincoln National Forest, 1941.

Discussion.—This species is characterized by its semicostate ornamentation and widely subpentagonal form. It is most suggestive of *Wellerella* which is common in many parts of the Pennsylvanian. It differs from that genus, however, in its exterior expression in having a shorter and less prominent beak, in having less deeply sulcate pedicle valves and more subdued costation. No other species of *Stenoscisma* is now known from the Pennsylvanian of the United States.

Stenoscisma bowsheri suggests Grabau's genus *Nantanella* from the Maping limestone of China, but that genus, although externally like the American species in form and ornamentation, differs in having a narrow sulcus on the umbo of the brachial valve. Grabau attaches considerable importance to this small feature and is probably correct in arguing that it is a stock different from those stenoscismas that do not have it. Furthermore, the figured interior details of *Nantanella* are different from those of the American species.

No described American Permian species of *Stenoscisma* are like *S. bowsheri*. Perhaps the nearest one is *S. hueconiana* (Girty, 1929), from the Hueco limestone of west Texas. The two, however, are actually quite different. The Hueco species is larger than the Pennsylvanian species and the costae extend farther toward the beak, although the beak itself is smooth

Genus OLIGOTHYRINA, n. gen.

Small, with convex valves, ovate in outline; anterior commissure intraplicate; posterior half to three-quarters smooth, anterior half to quarter thrown into a few strong plications. Pedicle valve with a small oval, submesothyrid foramen; dental plates absent. Brachial valve with socket plates attached to wall of valve, short and small; descending lamellae attached to anterodorsal side of socket ridges; descending lamellae subparallel, wide; crural processes

located well forward near the transverse band; transverse band narrowly arched, broad.

Type species.—*Oligothyrina alleni* Cooper, n. sp.

Discussion.—This genus is characterized by its interior characters and the type of exterior folding. The interior is notable for the lack of dental plates in the pedicle valve and the lack of a hinge-plate. The simple loop in the brachial valve widens only slightly anteriorly.

This genus is suggestive of *Notothyris* at first glance but is different from that genus in the character of its loop and hinge-plate. *Notothyris* does not have dental plates in the pedicle valve but unlike *Oligothyrina* it is provided with a perforated hinge-plate in the brachial valve and the loop is generally wider anteriorly rather than with subparallel descending lamellae as in the New Mexico shell.

The genus with interior details closest to those of *Oligothyrina* is *Pseudodielasma* Brill (in Newell, 1940). This genus is not provided with dental plates in the pedicle valve and its cardinalia are similar to those of *Oligothyrina*. The loop however is wider anteriorly than it is at its place of origin and the transverse ribbon is narrow and bowed anteriorly at its middle. Although the interior of *Pseudodielasma* is similar to that of *Oligothyrina* the exterior folding is quite different. Brill describes the pedicle valve of *Pseudodielasma* as having an abscure fold and the brachial valve a shallow sulcus. Specimens of *Pseudodielasma* from the Coleman Junction limestone may have a sulcus on both valves, that of the pedicle valve being the stronger and the anterior commissure definitely plicate even in cases where the sulcus is visible in both valves. In such cases the specimen is bilobate anteriorly. Brill's holotype appears to have a sulcus on each valve but a nearly rectimarginate commissure. No plications appear at the anterior of *Oligothyrina*. The folding is thus quite different from that of *Oligothyrina*. In this genus the brachial valve has a sulcus and the commissure has a major wave in the direction of the pedicle valve. The brachial sulcus however is modified by the appearance of a short median costa. In the pedicle valve the fold has a corresponding short but deep sulcus. This is the intraplicate condition shown by Thomson (1927, p. 58).

Specimens of *Oligothyrina* have appeared in the silicious residues from the Word formation in the Glass Mountains. One species and a subspecies already described from the Guadalupe Mountains appear to belong to this new genus: *Notothyris schuchertensis* Girty and *N. schuchertensis ovata* Girty.

OLIGOTHYRINA ALLENI, n. sp.
Pl. 61,C, fig. 33–41

Shell small, slightly longer than wide, oval to subpentagonal in outline; sides rounded; greatest width located at about the middle. Anterior margin nearly straight. Anterior commissure intraplicate. Surface marked only by concentric growth lines and short costae restricted to the anterior third.

Pedicle valve moderately convex in lateral profile and with the greatest curvature in the umbonal region; anterior profile strongly arched. Umbo narrowly swollen, the swelling continuing anteriorly to the middle which is moderately inflated. Flanks convex and steep. Fold low, defined only at the front third. Anterior median half of valve marked by a narrow, shallow sulcus that indents anterior commissure and corresponds to a median brachial costa. Beak small, incurved, erect; foramen small, elongate elliptical, submesothyrid. Interior devoid of dental plates.

Brachial valve shallower than the pedicle valve, gently convex in lateral profile and moderately convex in anterior profile. Umbonal and median regions swollen; flanks steep. Sulcus originating anterior to the middle, broad and shallow and occupied by a single prominent, subcarinate costa. Flanks bounding sulcus narrowly rounded to form two costae. Interior with divided hinge-plate; inner socket ridge strong; crura originating on dorsal side of crural bases. Loop short, with subparallel descending lamellae and thick transverse band.

Measurements in mm.—	length	brachial length	width	thickness
Holotype 124409a	5.4	4.8	4.9	3.3
Paratype 124409b	5.0	4.4	4.4	3.5
Paratype 124409c	4.8	4.5	4.1	2.9
Paratype 124409d	4.5	4.1	3.8	2.7

Types.—Holotype USNM 124409a; figured paratypes: USNM 124409e-g; unfigured paratypes: USNM 124409 b-d.

Horizon and locality.—Magdalena formation (30–40 feet below top), ⅛ mile south of Old Juniper, from a small draw which crosses road, center E½, SW¼ sec. 25, T. 19 S., R. 11 E., upper Grapevine Canyon, Sacramento Mountains, Otero County, New Mexico. Forest Service Map of Lincoln National Forest, 1941.

Discussion.—This little species is characterized by the complicated folding at the anterior. Of described species *N. alleni* is most like *Notothyris schuchertensis* Girty, which is probably congeneric with the Magdalena species. *Notothyris schuchertensis* comes from the Permian (Capitan) limestone of the Guadalupe Mountains, Texas. Although it is a small species, it is nevertheless about 1½ times the size of *O. alleni* but has similar proportions. The two differ conspicuously however in the stronger coastae and deeper sulcation of the brachial valve of *O. alleni*. The New Mexico species is a much less slender form than *N. schuchertensis ovata* Girty which occurs with *N. schuchertensis*.

Family CARDIARINIDAE, n. fam.
Genus CARDIARINA, n. gen.

Minute, heart-shaped in outline; biconvex; anterior commissure rectimarginate to gently sulcate; surface smooth; shell substance impunctate. Pedicle valve with elongated beak; foramen round, apical, submesothyrid; symphytium(?) a flat plate not showing a suture. Lateral margins just anterior to beak excavated. Interior with long nearly divergent dental plates that flare anteriorly to form an indistinct ridge that loops around the excavated area. Teeth small, longitudinally narrow, attached to the inner side of the dental plates just anterior to the anterior end of the symphytium(?).

Interior of brachial valve with narrow, slit-like sockets bounded by thin outer socket ridges and high, long, stout inner socket ridges; space between socket ridges forming a pit in the notothyrial thickening, the pit probably being the site of diductor attachment; median septum absent, but its function served by the strong median carina created by the deep sulcus of the exterior. Muscle scars not discernible. Outer socket ridge extended anteriorly around the downfolded lateral margins which are extended ventrally and may have served in lieu of crura.

Type species.—*Cardiarina cordata* n. sp.

Discussion.—Although this is a genus of minute forms it makes up for the lack of size by its great interest because it presents features which are unique among known brachiopods. The form of the shell with its exaggerated heart-shape is distinctive. This unusual form for a brachiopod is produced by the elongation of the beak and the fact that both valves are provided with a median sulcus in their anterior halves. The elongation of the beak is not as great proportionally to the body of the valve in *Cardiarina* as it is in the Cretaceous genus *Lyra* or the Silurian triplesiid *Onychotreta*, but it is nevertheless considerable. The elongation produces peculiarities in the deltidial and dental plates.

The foramen is a minute, round, apical opening at the end of the somewhat tubular beak. The tubular form is produced by divergent and erect dental plates which are roofed over by a single flat or slightly concave plate. Not one of the specimens examined showed any indication of this plate having been formed of two pieces. It is therefore doubtfully referred to as a symphytium.

The dental plates already alluded to are unusually developed. They extend from the foramen anteriorly and line the narrowly infolded sides of the elongated beak. They extend from the foramen, widening anteriorly to the point at which the teeth are attached. They then narrow again as they extend to about the valve middle. Here their ends flare laterally and are extended nearly to the margin as a low, often indistinct ridge. They are erect throughout their extent.

The teeth are as remarkable as the dental plates. They appear as narrow, elongated plates with medially curved articulating points where the dental plates are widest apart. This is just anterior to the anterior end of the sympytium(?). The teeth are strengthened by ridges that extend posteroventrally along the side of the dental plate.

No trace of the muscles of the pedicle

valve was observed in any of the numerous interiors of this valve available for study.

The cardinalia of the brachial valve are unusual. The sockets are elongated slits formed by the thin outer socket ridge and a thick inner socket ridge. The outer socket ridge flares slightly to make the socket and this flared part appears on the exterior as a small swelling. The inner socket ridge is a laterally compressed, erect plate that protrudes in a ventral direction beyond the margin of the outer socket ridge. This plate is braced or cemented to the inner wall of the valve where it is very narrow. No crura extend from the socket ridge and they were not seen in any of the numerous interiors examined. Between the inner socket ridges at the extreme posterior of the shell is a thickening which welds these structures together and which strengthens the valves at this point. Between the socket ridges and on the surface of the thickening between them is a pit that probably served as the place of attachment of the diductor muscles from the pedicle valve. In a few specimens the thickening appears to be further strengthened by a septal ridge, but this is not extended anteriorly. The only median strengthening of the valve is the narrowly rounded to carinate ridge produced by the deep and narrow sulcus of the exterior.

The site of adductor attachment is clearly in the narrowed posterior half of the brachial valve. A depressed area can be observed at this point, but it was impossible to individualize any of the scars.

Parathyridum.—The most unusual features of *Cardiarina* are the excavations and openings into the valve on the sides. No other known brachiopod has this feature although a new genus from the Permian of the Glass Mountains has a similar but not identical feature. The openings have caused modifications of both valves, those of the brachial valve, possibly having profound influence on the internal structure, may have caused disappearance of the crura.

In the pedicle valve the sides are narrowly folded. This folded part continues anteriorly along the dental plates to the point where they terminate. Although no clearly defined beak ridges are present, the lateral edge of the shell from about the anterior end of the symphytium(?) to the valve middle appears to correspond to the beak ridge. If this be true, the part of the pedicle valve so located has been folded medio-ventrally to the valve floor, almost eliminating the umbonal chambers. The thickening on the valve floor curving from the anterior end of the dental plates to the lateral margins defines the extent of this down-folding of the pedicle valve. A corresponding fold, but of a different kind, exists in the brachial valve.

In the brachial valve the sides are depressed from the bulge produced by the socket nearly to the valve middle. This produces a deep bend in the lateral margin, the margin from the socket bulge extending directly anteriorly, then abruptly bending laterally to join the narrowly rounded curving margin. The depression is deep on the outside and forms two big swellings internally. The narrowly curving edge of the depression fits around the curving ridge in the pedicle valve from the end of the dental plates to the lateral margin in the brachial valve.

In the articulated valves the parathyridium is deep and probably served as intake for food-bearing currents. This suggests the possibility that the deep infolds of the brachial valve served, at least in part, as the support of a simple schizolophus lophophore.

Classification.—It is difficult to place *Cardiarina* satisfactorily in the present scheme of classification. The form of the shell, elongate beak and deep bilobation suggest relationship to the Rhynchonellacea. This assignment is further strengthened by examination of the interior. Strong dental plates are a common feature of the Rhynchonellacea, few rhynchonellids being without them. Inside the brachial valve the strong inner socket ridges and their extension beyond the sockets is again suggestive of the Rhynchonellacea, the lack of crura being a high specialization. No known family of the Rhynchonellacea will receive these little shells; consequently, the family Cardiarinidae is here created to receive them. It is characterized as follows: Rhynchonellacea having an apical foramen, elongated beak, strong inner beak ridges, no crura and an elaborate parathyridium.

Enemies.—It is interesting here to note that many of the specimens examined bear a small round hole located in any part of the exterior except the beak (Pl. 61, fig. 1). This small hole suggests a gastropod boring. Many small gastropods occur in the siliceous residues with *Cardiarina* and one or more of them is probably responsible for the boring.

CARDIARINA CORDATA n. sp.

Pl. 61,A, fig. 1–19; Text-fig. 1C, no. 16–23

Shell attaining a length slightly less than 2 millimeters, valves subequally convex, the brachial valve being slightly the deeper; posterolateral margins gently concave, lateral and anterolateral margins narrowly rounded; anterior margin deeply indented medially. Lateral view with deep excavation just anterior to beak.

Pedicle valve with moderately convex lateral profile and a broadly but gently convex anterior profile; median region swollen to produce a humped appearance in the profiles; sulcus originating at about the middle, not always clearly defined, shallow and narrow. Flanks bounding sulcus moderately swollen.

Brachial valve gently convex in lateral profile and with the greatest convexity in the umbonal region; anterior profile gently convex; beak and umbo somewhat elongated and narrowed. Sulcus originating at the middle, narrow and deep, forming a reentrant in the anterior margin. Flanks bounding sulcus narrowly rounded and swollen; lateral and medial slopes steep. Recess just anterior to beak deep.

Interior as defined for the genus.

Measurements in mm.—	length	brachial length	width	thickness
Holotype 124411a	1.7	1.3	1.8	1.1?
Paratype 124411b	1.6	1.2	1.4	0.7
Paratype 124411e	1.7	1.3	1.6	0.8
Paratype 124411g	1.5	1.1	1.5	0.8
Paratype 124411h	1.8	1.4	1.75	0.8

Types.—Holotype: USNM 124411a; figured paratypes: USNM 124411b-f,i,j; unfigured paratypes: 124411g,h,k,l.

Horizon and locality.—Magdalena formation (30–40 feet below top), ½ mile south of Old Juniper, from a small draw which crosses road, center E½, SW¼ sec. 25, T. 19 S., R. 11 E., upper Grapevine Canyon, Sacramento Mountains, Otero County, New Mexico. Forest Service map of Lincoln National Forest, 1941.

Discussion.—No other species of this genus is known to which this one can be compared.

REFERENCES

BELANSKI, C. H., 1928, Pentameracea of the Devonian of northern Iowa: Univ. Iowa Studies, vol. 12, n. ser., 148, no. 7, p. 24–34.

BRILL, K. G., JR. *in* Newell, N. D., 1940, Brachiopods of the Whitehorse Sandstone, Geol. Soc. Am. Bull., vol. 51, p. 316–319.

GEORGE, T. N., 1927, Studies in Avonian Brachiopoda: II. The Genus *Camarophoria:* Geol. Mag., vol. 64, no. 5, p. 193–201.

GIRTY, G. H., 1929, New Carboniferous invertebrates—II: Wash. Acad. Sci., Jour. vol. 19, no. 18, p. 406–415.

GRABAU, A. W., 1934, Early Permian fossils of China, Pt. 1. Early Permian brachiopods, pelecypods and gastropods of Kweichow [sic]: Palaeont. Sinica, ser. B, vol. 8, fasc. 3.

——, 1936, "Early Permian fossils of China, Pt. 2. Fauna of the Maping limestone of Kwangsi and Kweichow [sic]: Palaeont. Sinica, ser. B, vol. 8, fasc. 4.

KNIGHT, J. B., 1933, The location and areal extent of the Saint Louis Pennsylvanian outlier: Am. Jour. Sci., vol. 25, p. 25–48, 166–178.

LICHAREW, B., 1936, Über einige oberpaläozoische Gattungen die *Terebratulacea* aus Eurasien: Moscow Univ. Pub. Lab. Paleont., Problems of Paleontology, vol. 1, p. 263–273.

THOMSON, J. A., 1927, Brachiopod morphology and genera (Recent and Tertiary): New Zealand Board of Sci. and Art, Manual 7.

WELLER, STUART, 1914, The Mississippian Brachiopoda of the Mississippi Valley Basin: Geol. Survey Illinois, mon. 1, p. 169–175.

MANUSCRIPT RECEIVED JULY 25, 1955.

(*See page 530 for explanation of Plate 61.*)

Explanation of Plate 61

A. *Cardiarina cordata*, n. sp.

Fig. *1–19—1–5*—Respectively brachial, side, pedicle, posterior and anterior views of a complete specimen, ×8, paratype USNM 124411b; *6–9*, respectively posterior tilted, side tilted, brachial and pedicle views, ×8, of the holotype, USNM 124411a; *10,11*, brachial and side tilted views of the holotype showing flat plate and deep parathyridium, ca. ×15; *12,13*, pedicle and brachial views of a specimen smaller than the holotype, ×8, paratype USNM 124411i; *14*, specimen tilted to the side to show apical foramen and parathyridium, ×8, paratype USNM 124411j; *15,16*, side and interior views of a pedicle valve. ×10, showing dental plates and teeth, paratype USNM 124411f; *17*, another pedicle interior showing dental plates, ca. ×15, USNM 124411c; *18,19*, interior and posterior views of the brachial valve showing bulging sockets bounded by thin outer socket ridges and the thick inner socket ridges, ca. ×15, paratype USNM 124411d.

Magdalena formation (30–40 feet below top), ⅛ mile south of Old Juniper, center E ½, SW ¼ sec. 25, T. 19 S., R. 11 E., upper Grapevine Canyon, Sacramento Mountains, Otero County, New Mexico.

B. *Psilocamara renfroarum* n. sp.

Fig. *20–30—20*, Brachial view of the holotype, ×1, USNM 124412a; *21–25*, respectively brachial, anterior, side, pedicle and posterior views, ×2, of the holotype, showing angular tongue and smooth surface; *26–30*, respectively anterior, posterior, brachial, side, and pedicle views of another complete specimen, ×3, paratype USNM 124412b.

Pennsylvanian (Capps formation), roadcut on Texas Highway 148, 5.7 miles north of the junction with Texas 199, north-northwest of Jacksboro, Jack County, Texas.

31,32—Anterior and brachial views of a small specimen, ×3, figured specimen USNM 124415.

Pennsylvanian (Henrietta formation, Fort Scott member), Pershing Avenue and Cleveland Walk, University City, St. Louis County, Missouri.

C. *Oligothyrina alleni*, n. sp.

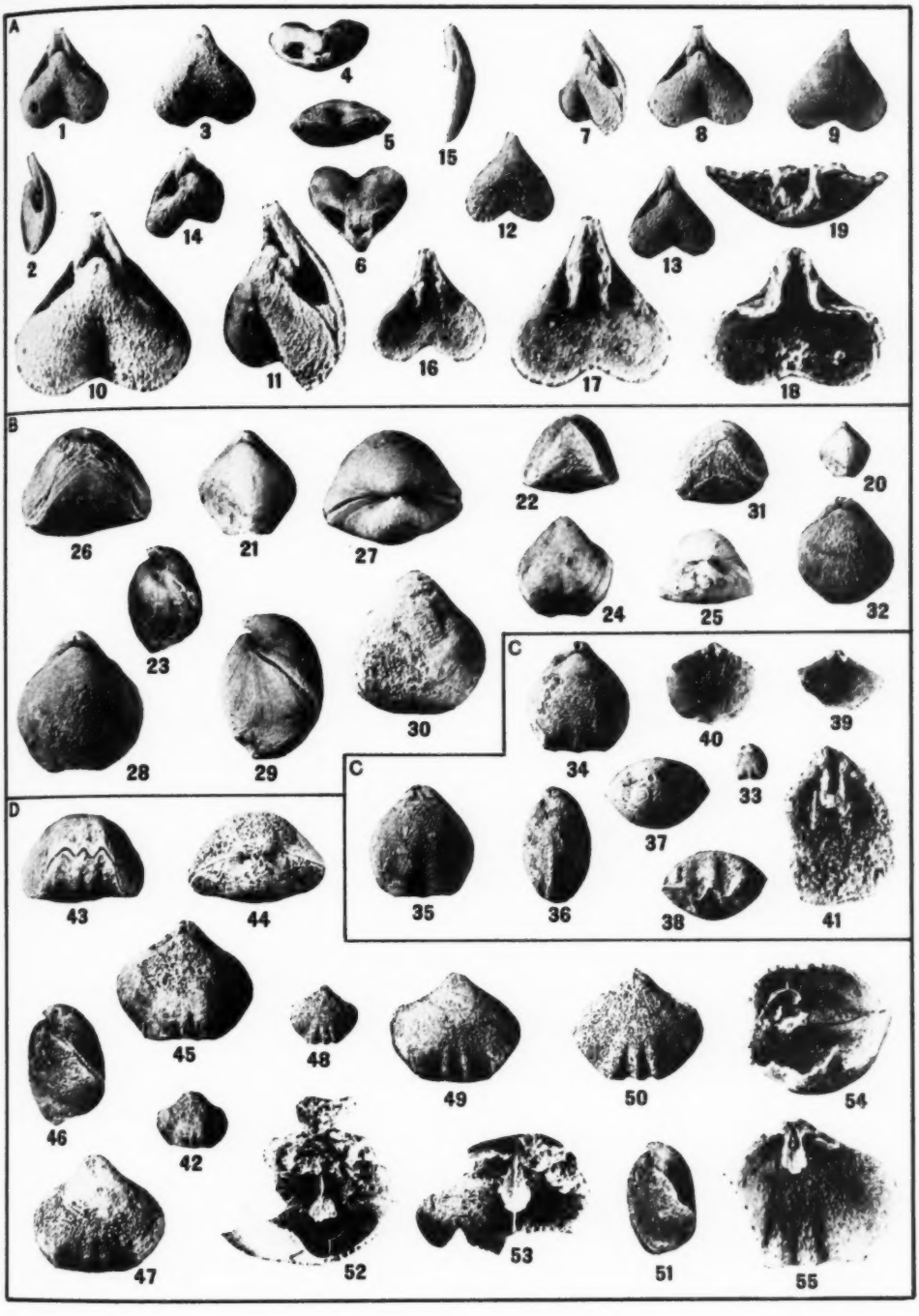
Fig. *33–41—33*, Brachial view of the holotype, ×1, USNM 124409a; *34–38*, respectively brachial, pedicle, side, posterior and anterior views of the holotype, ×2, showing costation at front and strong median costa in sulcus of brachial valve; *39*, imperfect pedicle valve tilted to show umbonal chamber lacking in dental plates. ×4, paratype USNM 124409e; *40*, interior of an imperfect brachial valve showing divided hinge-plate, ×4, paratype USNM 124409f; *41*, interior of another brachial valve showing the slender loop, ×6, paratype USNM 124409g.

Horizon and locality same as A.

D. *Stenoscisma bowsheri*, n. sp.

Fig. *42–55—42*, Brachial view of the holotype, ×1, showing anterior costae and smooth posterior half, USNM 124408a; *43–47*, respectively anterior, posterior, brachial, side and pedicle views of the holotype, ×2; *48*, brachial view of a paratype, ×1, more strongly costate than the holotype, USNM 124408b; *49–51*, respectively pedicle, brachial and side views of the preceding paratype ×2; *52,53*, two views from the anterior showing the cardinalia, ×3, paratype USNM 124408g. The brachial valve is on the upper side, and the spondylium below; *54*, another interior showing the cardinalia including one of the crura, ×3, paratype USNM 124408h. In this view the pedicle valve is on the upper side and the cruralium on the lower side. Note the broad spondylium. *55*, Interior of a brachial valve tilted to show the cruralium, ×3, paratype USNM 124408i.

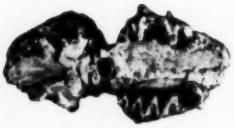
Horizon and locality same as A.


A
1
3
4
5
15
7
8
9
2
14
6
12
13
19
10
11
16
17
18
B
26
21
27
22
31
20
24
25
32
23
28
29
30
C
34
40
39
33
37
35
36
38
41
D
43
44
45
48
49
50
54
46
42
47
52
53
51
55

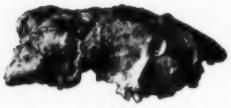
1

2

5

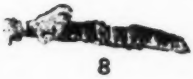


4

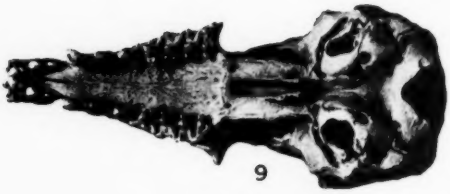


6

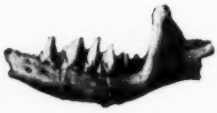
3



8

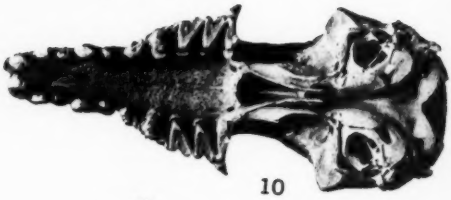


9

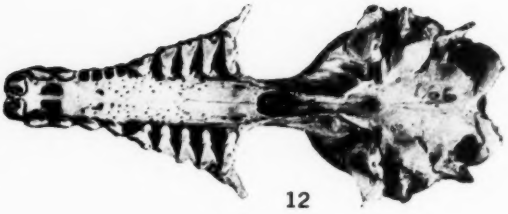


7

11

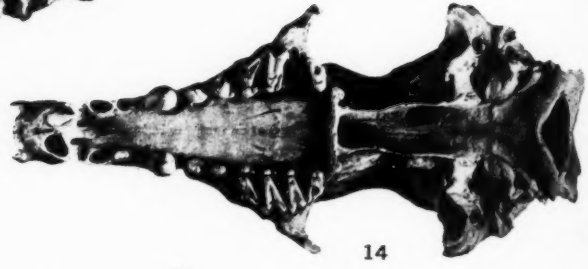


10

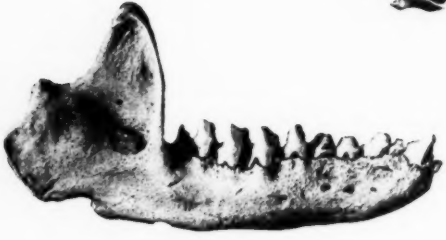


12

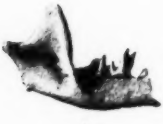
13



14



15



16

17

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 531–541, PL. 62, 2 TEXT-FIG., MAY 1956

A NEW INSECTIVORE FROM THE OLIGOCENE OF THE WIND RIVER BASIN, WYOMING, WITH NOTES ON THE TAXONOMY OF THE OLIGOCENE TENRECOIDEA[1]

JEAN HOUGH
U. S. National Museum, Washington, D. C.

ABSTRACT—A new genus and species of tenrecoid insectivore, *Oligoryctes cameronensis*, discovered by J. D. Love in Oligocene strata near Cameron Spring, Wyoming, is described and the classification of the Oligocene Tenrecoidea reviewed. It is concluded that the reference of *Apternodus* to the Solenodontidae is in error and that the family Apternodontidae Simpson, 1931, should be revived.

INTRODUCTION

IN 1944, J. D. Love, C. O. Johnson, and H. A. Tourtelot collected a number of vertebrate fossils from the south side of a badland butte about a mile northeast of Cameron Spring, Wyoming, Center W line, SE¼NW¼ sec. 1, T. 32 N., R. 90 W., Fremont County, Wyoming. The butte is part of an extensive badland area a few miles northwest of Beaver Divide. Brief collecting trips made by the writer and others following the initial discovery of the locality by Love have yielded an abundant fauna very similar to that of Pipestone Springs, Montana. The rodent *Cylindrodon* cf. *C. fontis* Douglass is particularly common, also *Titanotheriomys* sp., *Leptomeryx esulcatus* Cope, *Leptomeryx mammifer* Cope, *Mesohippus hypostylus* Osborn and titanotheres. One brontothere specimen (a complete skull, mandible, and some limb bones) seems to be *Menodus heloceras* Osborn. A partial skull and mandible referred by Osborn to this species has been collected from the channel fill of Beaver Divide. The Cameron Spring fauna, which will be described as a whole in a later paper seems closely comparable with the lower Oligocene faunas of the western Beaver Divide localities and of the same age, although probably not from the same facies as the fauna from Pipestone Springs, Montana.

A small insectivore skull and jaws, collected by J. D. Love, is of special interest, because it belongs to the Tenrecoidea and is closely similar in dental characters to *Apternodus*, the more common tenrecoid of the North American Oligocene. The small size of this insectivore and certain characters of the skull and dentition are sufficiently different from those of *Apternodus* to indicate that there was a greater variety and adap-

[1] Publication authorized by the Director, U. S. Geological Survey.

EXPLANATION OF PLATE 62

All specimens from the U. S. National Museum collections.

FIG. *1,2—Centetes ecaudatus* (Schreber), immature specimen, ventral view of the skull, lateral view of left lower jaw, ×1.1.
3—Oryzorictes tetradactylus Milne-Edwards & A. Grandidier, left lateral view of mandible, ×2.2.
4–8—Oligoryctes cameronensis, n. gen., n. sp., ventral view of skull, inner view of left lower jaw, lateral view of skull, lateral view of left lower jaw, crown view of lower jaw, all ×2.2.
9—Oryzorictes tetradactylus Milne-Edwards & A. Grandidier, ventral view of skull, ×2.2.
10,11—Microgale (*Nesogale*) *dobsoni*, Thomas, ventral view of skull, left lateral view of mandible, ×2.2.
12,13—Potamogale velox Du Chaillu, ventral view of skull, right lateral view of mandible, ×2.2.
14,15—Solenodon cubanus Peters, ventral view of skull, right lateral view of mandible ×2.2.
16.17—Micropternodus sp., lateral view of fragmentary right lower jaw, ×2.2.

tive radiation of this type of insectivore in the Oligocene than has been supposed.

MODERN TENRECOIDEA

Families of modern tenrecoids.—The living Tenrecoidea are a very restricted group composed of three families, with only a few genera widely separated geographically and highly specialized for particular modes of life. Although they have similar cheek teeth they differ in many details of the soft anatomy, cranial characters, and adaptation of the limbs and skeleton.

The most numerous and diversified family the Tenrecidae, inhabit Madagascar where they have taken over a variety of ecological niches occupied in other areas by other types of insectivores or small carnivores. The family Potamogalidae inhabits equatorial west Africa. There is only one genus, *Potamogale* a semiaquatic form, which lives along stream banks feeding on water beetles, crayfish, and small fish. The only New World family, the Solendontidae, also is monogeneric. The species of the single genus *Solenodon*, inhabit the mountainous parts of Cuba and Haiti in regions so remote that their habits are little known.

Dentition.—The zalambdodont type of dentition, which is common to the group, is one of the simplest possible modifications of the reptilian cone. The anterior premolars are simple cones. In the upper teeth P^3 usually consists of a high median cusp flanked by anterior and posterior cusps of varying heights and sharpness—but never as broad or high as the median cusp. In the molars, the median cusp becomes internally placed forming the apex of a trigon, the outer angles of which are formed by the para- and metastyles. Internally and usually somewhat anteriorly of the apical cusp the internal cingulum forms a cusp or cusps. The development of these internal cusps, and to a lesser degree the form and position of the apical cusp, differs widely in the various genera.

In the Tenrecidae the basal internal cingulum never forms a distinct cusp. In *Centetes* (Pl. 62, fig. 1,2) one of the larger forms with strongly developed piercing canines, the cingulum forms a broad shelf anterior and posterior to the median cusp and almost on a level with it. The apical cusp functions as a protocone, i.e., it fits into the basin of the talonid of the lower molars. In *Hemicentetes* there is no cingulum to the upper molars and no talonid to the lower molars. In the very small tenrecids *Microgale cowani* and *Microgale* (*Nesogale*) *dobsoni* (Pl. 62, fig. 10,11), the cingulum forms a low flaring heel surrounding the base of the apical cusp. It does not function as a protocone. The talonid of the lower molars is extremely reduced. Another of the smaller genera, *Oryzorictes* (Pl. 62, fig. 3,9) has a sharp slender cusp on the internal basal cingulum of the upper molars. The talonid of the lower molars is transversely short and deep and bounded posteriorly by a sharp cusp.

In *Potamogale* (Pl. 62, fig. 12,13) the cingulum reaches its greatest development forming an internal cusp, which is single, sharp pointed, and almost as high as the apical cusp. It functions as a protocone fitting into the talonid of the lower molars. The trigon of the upper molars is short and broad, bringing the apical cusp to almost a median position. The talonids of the lower molars are broad and deep, bounded posteriorly by a low ridge.

In *Solenodon* (Pl. 62, fig. 14,15) the internal cingulum forms two cusps; the anterior one is the higher and sharper of these, but neither is nearly as high and sharp as the apical cusp. The cingular cusps do not function as a protocone. The apical cusp fits into the talonid of the lower molars, which is not strongly developed. The trigon of the upper molars is relatively long and narrow.

Premolar development differs also in the various families. In *Centetes* P^3 is the largest of the cheek teeth and, although not molariform, is complicated. There is a large median cusp, very high and sharp in unworn teeth, with a small parastyle situated some distance anteriorly, and a metacone of similar size directly anterior and external to the parastyle. The basal cingulum is entirely anterior in position and well developed. All the remaining cheek teeth, except M^3 are of equal size. M^3 is almost as large but narrower and transversely placed. *Microgale* and *Oryzorictes* do not have the enlargement of P^3 characteristic of *Centetes*.

In *Potamogale* P^3 is small with a high

median cusp, well-developed anterior and posterior styles and a heel-like cingulum lower than that of the molars but very similarly shaped. P^4 is molariform and the smallest of the cheek teeth. These increase in size to M^2, which is at the angle of the tooth row. M^3 is narrow and obliquely placed.

In *Solenodon* P^3 is a large, blunt cone almost as broad as long with little stylar development. There is almost no internal cingulum. P^4 is molariform. M^1 is the largest molar and forms the angle of the tooth row with both M^2 and M^3 reduced.

The variation of the canines and incisors although also marked from genus to genus fall into two general patterns related to the habits of the animals. In the one type the median incisors are very much enlarged and elongated. *Solenodon* represents the extreme of this type. The broad shovel-shaped incisors directed downward and backward from the overhanging snout form very effective digging instruments. In the smaller Tenrecidae, the Oryzorictinae, the median incisors are also elongated and extend well below the tips of the other teeth, but they are not particularly stout and are not directed backward. *Potamogale* is intermediate between these two extremes. The median incisors are long, stout, and chisel shaped but not broad as in *Solenodon* nor directed posteriorly.

The other type of canine and incisor dentition is characteristic of *Centetes*, *Hemicentetes*, and *Ericulus*. In these forms the first and second incisors are slender and short with a posterior basal cusp. The canines are very large, one-rooted, sharp-pointed teeth separated from the lateral incisors by a long diastema that is hollowed out into a groove for the lower canine.

Homology of the cusps of zalambodont molar teeth.—The homology of the cusps of the zalambodont molar teeth has been the subject of much controversy. The apical (median) cusp has been regarded as a protocone homologous to the lingual cusp of the tri-tubercular molar (Gregory, 1910); an amphicone (fused para and metacone) which subsequently divides; a paracone homologous to the antero-lingual cusp of the tri-tubercular molars (Butler, 1937). Much of this difficulty seems to stem from differing theories as to the evolution of the mammalian molar. As was first pointed out by Wortman (1902) the premolars of all mammals including the zalambodont insectivores become more complex by the addition of cusps in a definite order:

> The first step in this advance in structure is usually the addition of a cusp to the posterior border in the form of a talon. The next is an internal cusp which arises from the cingulum and by gradual enlargement becomes the main internal cusp of the tritubercular crown.

If the cusps of the molars are added in a similar way—and there is no reason to suppose that there was a different type of evolution for premolars and molars—the antero-external cusp of the molar corresponds to the single median cusp of the simplest premolar and the main internal cusp to the enlarged cingular cusp of the premolar. The cusp terminology in present use however, does not reflect these relationships because of the influence of the Cope-Osborn theory of cusp rotation. According to this theory the tritubercular molar tooth developed from the simple reptilian cone by 1) the addition of cusps on either side the median cusp giving a linear arrangement, the "triconodont" stage and 2) the rotation of these cusps in such a way that the anterior and posterior cusps (paracone and metacone) become situated on the external margin of the molar crown, leaving the median cusp (protocone) at the lingual apex of the triangle. Plausible as this theory was when first proposed, virtually all paleontological evidence supports the premolar analogy theory, which is now generally accepted. Nevertheless, the cusps still bear the names proposed by Osborn. In the tritubercular molar of creodonts, carnivores and some insectivores such as *Ictops*, the names, although not properly expressing the true homologies of the respective cusps, have a certain congruence with the position of the cusps on the molar crown. In zalambodonts this is not the case. The crown is triangular, but the trigonid is formed from the much extended external stylar portion of the crown, often with distinct cuspules, the para- and metastyles and an apical cusp. From analogy with the premolars, this apical cusp clearly corresponds to the single median cusp of the simplest premolar and is

therefore a paracone. In some ancient zalambodonts such as *Paleoryctes* the apical cusp is double, forming a distinct metacone as well as the paracone. In all modern zalambodonts, and the known Oligocene genera the cusp is single, with at best a metacone feebly developed on the posterior slope of the paracone. The lingual cusp, when developed, corresponds to the cusp formed from the internal cingulum in the premolars and is therefore a protocone. As pointed out in the description of the modern tenrecoidea, however, this cusp does not always function as a protocone, and in some forms, ancient as well as modern, is hardly developed at all. The zalambodont molar therefore has a fundamentally different pattern than the tritubercular molar, and the cusp terminology carried over from the tritubercular type of tooth is hardly applicable. In this paper, to avoid confusion the cusps will be designated by position rather than homology.

Basicranial region.—The basicranial region differs as much in the three families as the dental characters. That of the tenrec (*Centetes*) is probably the most specialized. The basicranium is wide transversely and short, in contrast to the slim elongate mid-region of the skull. The most prominent features are the broad, concave, obliquely directed glenoid processes. These extend almost to the level of the occipital condyles. The mastoid is directed posterolaterally and seems a winglike extension of the occipital shield. The paroccipital processes are rod shaped and extend backward and downward beyond the condyle.

The basisphenoid is excavated into a pit just anterior of the base of the postglenoid processes, the roof of which is pierced by a foramen. The lateral descending processes of the basisphenoid form the postero-lateral margins of the pit, and extend posteriorly to cover the medial portion of the auditory cavity. There is a tympanic ring, small and oval in shape, but no real bulla. The basisphenoid processes almost meet the postglenoid processes in such a way that only a narrow strip of the tympanic cavity is left uncovered.

Microgale and *Oryzorictes* have much more normal types of auditory region. In these genera the basicranial region is longer antero-posteriorly than in *Centetes* and somewhat narrower. The glenoid fossa is directed transversely.The mastoid extends anteriorly to meet the external margin of the glenoid giving the auditory region a rectangular shape. Except for the opening of the external auditory meatus the auditory cavity is entirely encircled by the tympanic ring that is expanded to form a fragile, narrow inner margin of a bulla. The basisphenoid is very narrow between the auditory bullae and deeply excavated in the midline, but there is no pit. There are no lateral descending processes that form the medial portion of the bullae. The paroccipital processes are slender and posteriorly extended as in *Centetes* but because of the greater length of the basisphenoid do not extend beyond the occipital condyle.

The basicranium of *Potamogale* closely resembles that of *Microgale*, being practically a larger edition of it. The postglenoid processes are somewhat broader and stouter, the auditory bullae more completely ossified and thicker, the basisphenoid-basioccipital part of the basicranium more developed; the relations of the mastoid and paroccipital are the same, and the paroccipital processes, although somewhat more flattened, have essentially the same form and relationships to the surrounding parts of the skull.

In *Solenodon* the basicranium is relatively short and broad, but not nearly as much so as in *Centetes*. The postglenoid processes are strongly extended transversely with rudimentary zygomatic processes. The glenoid fossae are shallow with a posterior rim developed only medially. The mastoid is very small and united with the ecto-glenoid processes. There are no paroccipital processes. The basisphenoid is broad between the auditory cavities and has no lateral processes. There are no auditory bullae. The tympanics, when present, are oval rings that cover only the antero-lateral portion of the auditory cavity.

Relationships of the modern Tenrecoidea.—The very considerable diversity of adaptation within the Tenrecoidea is evident from the foregoing summary, which includes only characters useful in determining the affinities of the known fossil tenrecoids. Aside from the general pattern of the teeth and certain basic insectivore characters the

diversity would almost seem to be greater than the unity. According to Dobson (1882), however, there is a remarkable uniformity in the structure of the urinary and generative organs, and in such details of the soft anatomy as the distribution of the flexor tendons of the leg and foot. Butler (1937) in his discussion of the affinities of the zalambodonts, while pointing out the wide range of evolutionary grades in the modern genera, discusses also the resemblance of the dentition to that of the upper Jurassic Paurodontidae and suggests an ancestral relationship between the zalambodonts and Paurodontidae. He believes that the resemblances of the zalambodonts to other insectivores, when they are not merely primitive characters, are due to parallel evolution. It would seem, therefore, that the Tenrecoidea are a true genetic group of ancient origin, retaining many primitive features but adaptively diversified in response to the ecological niches available.

The Solenodontidae are structurally the most isolated. The characters of the soft anatomy and the auditory region are quite dissimilar to those of either the Tenrecinæ or the Oryzorictinae. This is possibly an example of evolutionary divergence, however, due to geographic isolation. The immature *Centetes* has an auditory region very like that of *Solenodon* and the characters of the dentition (e.g., the greatly enlarged incisors) are an exaggeration of features common to all of the Old World Tenrecidae.

OLIGOCENE TENRECOIDEA

Three genera of the Tenrecoidea are known from the Oligocene. Two of these, *Micropternodus* and *Clinopternodus* are represented only by lower jaws. Specimens of the third, *Apternodus*, are more numerous and complete and will be discussed first.

The genus *Apternodus* was established by Matthew (1903) on *Apternodus mediaevus*, represented by fragmentary lower jaws from Pipestone Spring, Montana. Matthew later described a virtually complete skull and mandible from Bates Hole, Wyoming, referring it to the same species (Matthew, 1903, 1910). Schlaikjer (1933) described a new species *A. gregoryi* based on a skull and mandible from the Brule formation of the Goshen Hole area, Wyoming, and later (Schlaikjer, 1934) redescribed Matthew's specimen from Bates Hole as a new species, *A. brevirostris*. Recently Galbreath (1951) has erected another species *A. illifensis* on a partial upper and lower dentition from the Horsetail Creek member of the White River formation of Logan County, Colorado. Fragmentary remains are also known from the Oligocene of Canyon Ferry, Montana, the Chadron formation near Orella, Nebraska and the Cook Ranch formation of Wood (1933), Beaverhead County, Montana.

The taxonomic history of *Apternodus* has been varied. Originally placed in the Tenrecidae by Matthew (1910) it was later separated as a distinct family, the Apternodontidae by Simpson (1931) and is now ordinarily classified with the Solenodontidae following Schlaikjer's arguments in favor of that relationship (Schlaikjer, 1933; Simpson, 1945).

It is not within the scope of this paper to assess the taxonomic or phylogenetic significance of these characters. As an introduction to the discussion of fossil forms, however, it is desirable to point out that certain variations are recurrent. Enlarged median incisors, as well as variations of the basal cingulum of the upper molars, high, low cuspate, noncuspate, divided and undivided, occur in several different groups and if the basis of classification used by Dobson (1882) is correct, were independently evolved. A ring-shaped tympanic is also present in all of the Tenrecidae, although in the Tenrecinae it is covered over by processes of the alisphenoid and basisphenoid. In the Solenodontidae the ring-shaped tympanic has the size and position of that of an immature *Centetes*. The smaller Tenrecidae, on the other hand, have a basicranial region resembling that of *Potamogale*.

Including an Oligocene species in a modern family usually requires considerable extrapolation, because in every instance Oligocene members of a phylogenetically erected family resemble certain members of other Oligocene families more than they do the modern members of the same family. Similarly, members of modern families can resemble members of other modern families more than they do the more primitive members of their own family. In such families as the Canidae or Equidae, where the evolu-

tionary history is well known and documented by numerous complete skulls and skeletons, a phylogenetic classification is undoubtedly the most natural and most informative. In the Insectivora, in which the evolutionary history is probably complex, and is obscure because of lack of specimens, placing an Oligocene genus in a modern family does not seem warranted unless there is a clear and certain morphological correspondence. To the writer such a clear and certain correspondence between *Solenodon* and *Apternodus* does not exist.

Schlaikjer (1934) admitted that the dentition of *Apternodus* resembled that of *Microgale* more than it did that of *Solenodon*. He thought, however, that he detected an incipient division of the internal basal cingulum of the upper molars into two cusps, and argued that this foreshadowed a development into the high partially twinned cusps of *Solenodon*. There is really no evidence in the teeth themselves for this assumption. Aside from the question of the reality of the division of the internal cingulum of *Apternodus* into two cusps, such a division could equally well foreshadow the condition in *Centetes*. In fact, the variation of the basal internal cingulum of *Apternodus* from species to species parallels that of the Tenrecidae in which *Hemicentetes* has no internal cingulum, *Oryzorictes* has a slender sharp internal cingular cusp much lower than the apical cusp but quite distinct, and *Microgale* has a cingulum developed into a crescentic heel.

The other characters in which Schlaikjer saw a special resemblance between *Apternodus* and *Solenodon* are also of dubious validity. The mandible of *Apternodus* agrees feature for feature with that of the Tenrecidae, whereas the mandible of *Solenodon* differs markedly from both. The shortness of the angle, which does not extend back as far as the condyle, and the strongly concave margin of the posteriorly extended base of the coronoid process are characters that set *Solenodon* apart from the Tenrecidae and *Apternodus*.

The basicranial region of *Apternodus* is, of course, unique because of the unusual development of the lateral face of the mastoid—

> which with adjoining parts of the exoccipital and squamosal bones forms a large lateral plane surface of rectangular form continuous with the outer end of the postglenoid process and bounded by four prominent heavy crests which project in a vertical plane. [Matthew, 1910]

The nearest approach to this structure in the modern Insectivora is actually the basicranial region of *Desmana moschata*. The similarity is obscured because the desman has an ossified bulla, but the relationships of the mastoid, exoccipital and squamosal are the same, and they form a large plate, not, however, facing entirely laterally as in *Apternodus* but more ventro-laterally so that the plate is exposed on ventral surface of the skull. Even aside from the unique development of the mastoid, the basicranium of *Solenodon* differs about as much from that of *Apternodus* as is possible within the limits of variation of the Tenrecoidea.

In *Solenodon* the basicranial region is short—in *Apternodus* it is proportionally long as in *Microgale* or *Potamogale*. In *Solenodon* there are no mastoid or paroccipital processes. The mastoid is united with the ectoglenoid in such a way that the outer margin of the auditory region slopes backward and inward from the postglenoid processes to the condyle. *Microgale* and *Potamogale*, in contrast, have well-developed mastoid processes and long, slender paroccipital processes directed posteriorly in such a way as to give a rectangular outline to the basicranial region.

There is no trace of a tympanic ring in any of the specimens of *Apternodus* nor any indication that the writer could find of its form or position. In any case, such a ring is characteristic of all of the Oryzorictinae as well as *Solenodon*. Moreover the tympanic ring in *Solenodon* is, as stated before similar to that of the immature *Centetes*. Therefore, its presence provides no proof of any special relationship to *Solenodon*.

One feature of the basicranium of *Apternodus* does agree with that of *Solenodon* and does differ from the Tenrecidae. This is the absence of the descending process of the basisphenoid, which in the Tenrecidae lies along the medial anterior margin of the auditory region and, when a bulla is formed, embraces the medial margin of the tympanic. There is a question, however, as to the taxonomic value of this character. It appears to the writer to be a feature in the

Insectivora on the order of the ossification of the bulla in the Carnivora, i.e., a development that takes place with the increasing ossification of the auditory region in several lines of descent. A tympanic wing of the basisphenoid is lacking in the Lepticidae but present in Erinacidae, which are generally considered to be descended from them.

Such a wing is apparently absent in the Paleocene *Palaeoryctes* (Matthew, 1913) and in *Apternodus* but appears to be present in *Oligoryctes*. It is present in all modern tenrecoids, but the degree of development varies from the slight, fragile processes of *Microgale* and *Oryzorictes*, which could be readily lost in a fossil skull to the stout flanges of *Centetes* firmly ankylosed to the main body of the basisphenoid. The writer believes, with Gregory (1910), that its absence in *Solenodon* is secondary. The condition may be comparable with that of the auditory bullae of the South African civet, *Nandinia*, which alone among living Viverridae has an unossified ectotympanic. Such a condition is also known in the fossil *Daphoenus*. Basing an ancestral relationship between *Solenodon* and *Apternodus* on this one feature would be like postulating such a direct relationship between the Oligocene *Daphoenus* and the modern *Naninia*.

Schlaikjer (1934) mentions a few other characters in which he saw a resemblance between *Solenodon* and *Apternodus*, such as the presence of a postorbital constriction, narrowing of the palate, etc., but, aside from their being doubtfully true (the writer, for example, fails to see much of a postorbital constriction in *Apternodus*), they are characters of *Potamogale* and cannot be said to have much taxonomic significance. In short, the morphology of *Apternodus*, as far as known—and of course this includes only cranial and dental characters—seems to ally it with the Tenrecidae, particularly the Oryzorictinae, far more than with *Solenodon*.

In the case of *Micropternodus* and *Clinopternodus*, comparison can be made only with lower jaws, none of which are complete. The resemblance between these lower jaws and the lower jaw of *Solenodon* has been considered sufficient to place them in the same subfamily.

Micropternodus (Pl. 62, fig. 16,17) is the better known form. The jaw is very small with a slender horizontal ramus and straight lower margin. The molar teeth have high compressed trigonids bounded by three high sharp cusps very close together but divided by a deep central valley. The internal cusp is much the highest of the three. The talonids are almost as long antero-posteriorly as the trigonids but are low. The basin of the talonid is very deep and bounded posteriorly by a sharp ridge. On P_4 to M_2 this ridge is about half the height of the internal cusp of the trigonid, on M_3 it is almost two thirds as high. The basins of the talonid are broad transversely and the ridge is divided into three small cusps, external, median and internal, on P_4 to M_2; and into two cusps on M_3. The antero-posterior length of the talonid increases from P_4 to M_3.

This type of cheek dentition is not exactly like that of any modern tenrecoid, but it comes closest to the milk dentition of a specimen of *Centetes acaudatus*, USNM 63315. There is the same high-pointed trigonid, the transversely broad, deep talonid bounded by a sharp ridge. The configuration of P_4 is notably similar in the two forms. There is a high median cusp flanked internally by a somewhat lower but distinct, sharp-pointed cusp, and anteriorly by a small sharp stylar cusp. The outer corner of the talonid is connected by a ridge with the postero-external corner of the trigonid. In *Micropternodus* the talonid on P_4 and the succeeding molars is somewhat longer antero-posteriorly, the ridge more sharply defined, and produced into cusps, which is not the case with the immature *Centetes*. Nevertheless the resemblance is marked.

The dentition also resembles that of *Potamogale* in much the same way as it does the immature *Centetes*, but the similarity of P_4 is not as marked.

Clinopternodus gracilis is represented by only one described specimen, which is a fragmentary jaw with the canine, P_3, P_4, M_1 Princeton Museum 14197. It is, according to John Clark (1937), very like *Micropternodus*, differing in that the teeth are more crowded and more compressed with the crowns recurved and procumbent. These characters do not afford any evidence of relationship with *Solenodon*.

Oligoryctes cameronensis (Pl. 62, fig. 4–8), as will be seen from the following description, is nearest to the Oryzorictinae of all modern

insectivores and shows no special affinities to *Solenodon*.

Recent collecting, especially an important ant-hill fauna discovered by Raymond Alf of the Webb School, Claremont, California, from the Chadron near Orella, Nebraska, and collections in Montana made by T. E. White from the Canyon Ferry area, and by the writer from the Cook Ranch type locality, Beaverhead County, show that the kind of insectivores described above were very widespread and more common than previously known. In short, there appears to have been a radiation of tenrecoid insectivores in the western part of the United States similar to that of the modern Tenrecidae in Madagascar but probably more diversified and widespread. For the present, this relationship seems best expressed taxonomically by placing all such forms in a separate family, the Apternodidae. This recognizes the lack of any character-for-character morphological correspondence of the North American Oligocene forms with any particular modern family.

It can be argued that a factor other than comparative morphology enters into the discussion of the relationship of *Apternodus* and *Solenodon*. *Solenodon* is the sole New World tenrecoid. All the other genera are from Africa and Madagascar. It would therefore be natural to postulate an ancestral relationship between tenrecoid insectivores of the mainland of North America and the islands of the coast of Central America even though the insectivores of the mainland are from a part rather remote from the six islands in question.

This speculation, interesting as it is, has no fossil evidence to support it and would not in itself be sufficient reason for including the Oligocene tenrecoids in the Solenodontidae. The writer tends to think that the ancestors of *Solenodon* did, in fact, reach the West Indies from the North American mainland rather than from Africa, the similarities of the Old World tenrecoids and *Solenodon* being an example of convergence. Nevertheless, some as yet unknown Miocene-Pliocene form—perhaps not even a zalambodont—seems more plausible as an ancestor than any of the known Eocene or Oligocene tenrecoids, which differ so markedly from *Solenodon* in important characters of the skull and dentition.

SYSTEMATIC DESCRIPTIONS

Order INSECTIVORA

Family APTERNODONITDAE

Genus OLIGORCYTES n. gen.

Type species.—*Oligoryctes cameronensis*, n. gen, n. sp.

Diagnosis.—The characters of the type species are the characters of the genus until other species are described.

OLIGORYCTES CAMERONENSIS, n. sp.

Holotype.—USNM 19909, skull and lower jaws. Basicranial region of skull incomplete. Incisors lacking in upper and lower jaws.

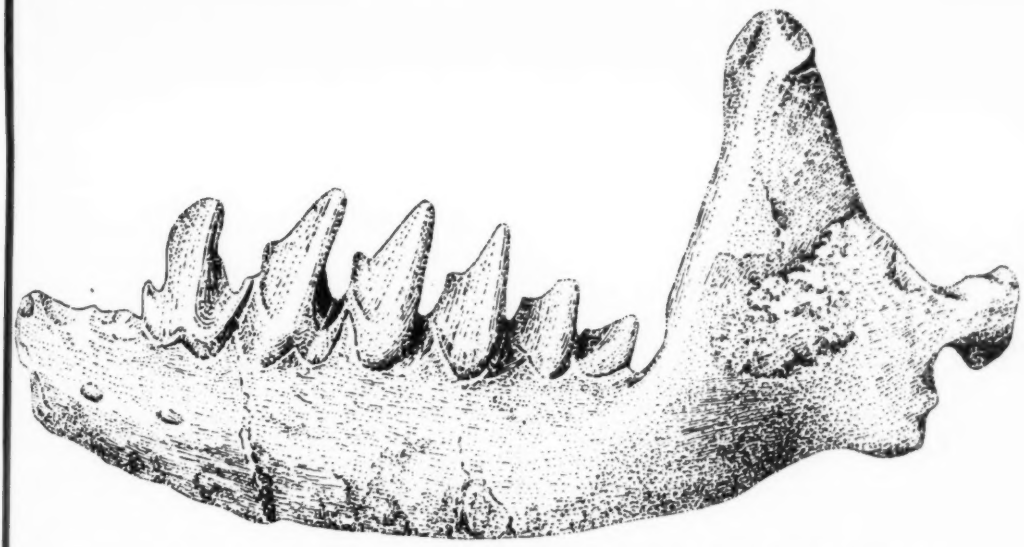
Horizon.—Lower Oligocene.

Locality.—Cameron Spring, Wind River Basin, Wyoming.

Diagnosis.—Very small insectivores with zalambdodont dentition similar to that of *Apternodus*. Basicranial region differs from that genus in having lateral descending processes of the basisphenoid, which embrace medially the small anterior bullae. P^3 longer antero-posteriorly than P^4 and as extended transversely, semimolariform with well-developed parastyle and metastyle; P^4 molariform. Mandible slender, alveolar margin straight, lower margin convexly curved. Coronoid process triangular, deflected laterally so that it is not in line with the tooth row. Condyle small, rounded, obliquely placed with little transverse extension. Central cusp of lower molars very high, slender, recurved, inclined posteriorly. P_3 with strong anterior cingular cusp and large talonid. Talonids of P_4, M_1, M_2 narrower but that of M_3 half the length of the tooth forming a broad basin bounded posteriorly by a prominent cusp.

Description and Discussion

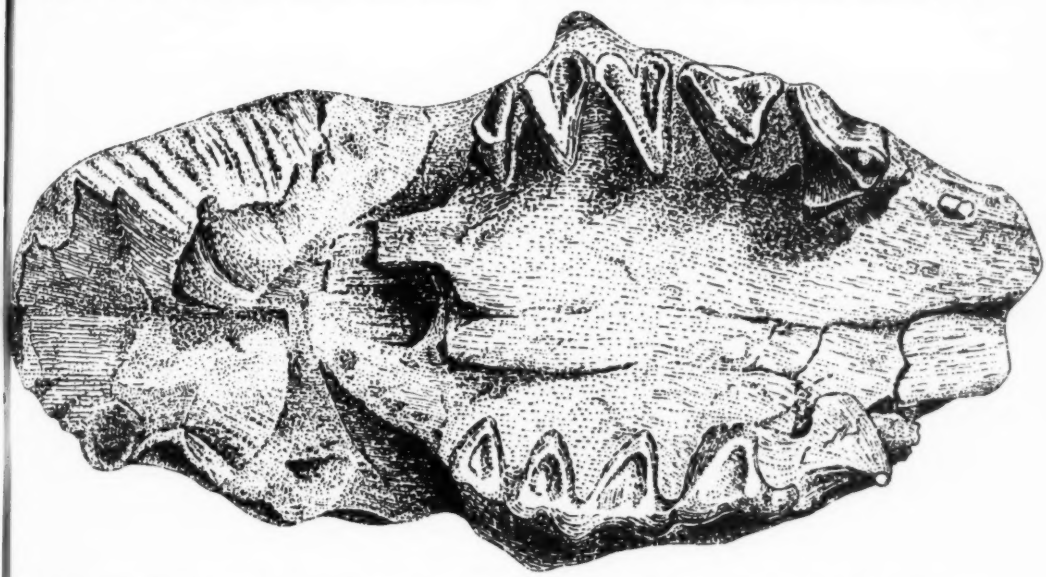
Upper dentition.—The upper incisors and canines are missing. P^2 is broken at the base but was apparently a small rounded tooth well separated from P^3. P^3 is the largest tooth in the molar series, longer antero-posteriorly than P^4 and as wide transversely. The three cusps that comprise the crown of the tooth are almost on a line. The paracone, which is the largest of these, is not much higher than the parastyle and is connected with it by a ridge. The metastyle is a low but distinct cusp separated from the paracone by a deep valley. The basal cingulum is extended medially, giving the



TEXT-FIG. 1—*Oligoryctes cameronensis* n. gen., n. sp., ventral view of skull, USNM 19909, ×2.

outline of the tooth a triangular shape but forms only a feebly developed cusp—hardly more than a rim at the base of the tooth.

P^4 is molariform, but the trigon is somewhat shorter and broader than in the succeeding molars. The elements of structure are the same. There is a high, conical, internal cusp, the paracone, which forms the apex of the trigonid. A ridge that slants forward, outward, and downward connects this cusp with a low cusp at the antero-external corner of the crown. This cusp is not the parastyle which in this tooth is separated from the main body of the tooth by a shelf formed of the basal cingulum. This shelf is well below the level of the crown of the tooth. It forms a trough bounded antero-externally by the slightly raised para-



TEXT-FIG. 2—*Oligoryctes cameronensis* n. gen, n. sp., lateral view of left lower jaw, USNM 19909, ×2.

style. The metastyle forms the postero-external corner of the trigonid and is extended more laterally than the antero-external corner so that the tooth is asymmetrical with the posterior half both longer and wider. A ridge connects the median cusp with the parastyle. Internally the basal cingulum forms a very low, cup-shaped rim at the base of the amphicone.

M^1, like P^4, is surrounded by a basal cingulum, which internally forms a low crescentic cusp and antero-externally a shelf. This shelf is somewhat narrower than that of P^4 and more nearly on a level with the trigonid. The parastyle is confluent with the low cusp at the antero-external corner and the metastyle developed very much as in P^4.

M^2 differs from M^1 in the greater development of the parastyle, which forms a raised ridge continuous along the anterior border of the tooth but especially prominent at the antero-external corner. The antero-external shelf is narrow and hardly visible from the crown view of the tooth. The internal cingulum is less developed and the metastyle is weak compared to that of M^1. This gives a different shape to the tooth, reversing the asymmetry so that the anterior half is the larger.

M^3 is a small tooth with the tendencies of M^2 exaggerated. The parastyle is very much more extended laterally than the metastyle, which is hardly more than the posterior slope of the amphicone. There is no distinct antero-external cingulum and the internal cingulum is only feebly developed.

Lower dentition.—The anterior teeth of the lower jaw are missing and the alveoli which remain difficult to interpret. Presumably, however, by analogy with *Apternodus brevirostris* Schlaikjer the very small stump of a tooth just anterior to P_3 is P_2. P_1 was never present. The larger alveolus next in line is the canine. A minute alveolus just anterior to that is about in the position of I_3 of *Apternodus brevirostris*. Presumably first and second incisors were present but have been broken off.

P_3 is as long antero-posteriorly as P_4 with the median conical cusp almost as high. The paraconid is low and slender but a distinct cusp in line with the median cusp. There is no metaconid. The talonid is broad and basin shaped with the posterior rim developed into a cusp. The cingulum does not surround the tooth, the internal surface being quite smooth. In P_4 of *A. brevirostris* the internal cingulum forms a raised rim at the base of the crown.

P_4 is molariform. Paraconid and metaconid are well developed, forming the usual trigonid. The heel is somewhat narrower than that of P_3 and not so strongly basined. M_1 and M_2 resemble P_4. The trigonid of M_3 is much reduced. The parconid and metaconid are almost equal in height and width, the median cusp forms an equilateral triangle. The talonid is large, forming at least half of the tooth. It is basined, with a high slender cusp at the posterior margin.

Skull.—The skull is about the size of that of the Oligocene shrew *Domina gradata* and rather resembles it in general contours. There is little similarity in that respect with any of the described species of *Apternodus*. The palate is broad, tapering almost to a point just anterior of P^2. The extreme anterior part is missing but probably consisted of a short and slender snout. The skull has been broken and mended in the midcranial region. There may have been some shortening in the process. Nevertheless, this area seems to lack the elongation common in the Tenrecoidea. The braincase is relatively large. There is no sagittal crest.

The facial portion of the maxilla forms a large sheet of bone bounding the orbits, which are deeper and more sharply defined anteriorly and antero-ventrally than in *Apternodus*. The large lachrymal foramen is situated anterior to the rim of the orbit. The infraorbital canal is long and narrow. This part of the skull in *Oligoryctes* differs from that of *Apternodus*, in which the orbital rim is narrow and twisted with the lachrymal foramen situated well within the margin of the orbit. The condition in *Oligoryctes* is more like that of the Tenrecidae, but there is no trace of an extension of the maxilla to form even the most rudimentary part of the zygomatic arch.

The palate is bounded posteriorly by a raised rim similar in form and position to that of *Centetes* and situated about the same distance from the last molar. The postglenoid part of the skull is broken, but judging from the shape and size of the condyle of the lower jaw the postglenoid processes were poorly developed and obliquely placed.

The basisphenoid is intact and has dis-

tinct, rather large descending processes, which embrace the antero-medial margin of the bulla. The bulla in the specimen is represented only by a cast, but from this cast appears to have been similar in shape and position to that of *Oryzorictes*. The lateral descending processes of the basisphenoid are also like those of *Oryzorictes*.

The posterior part of the skull has been badly damaged, the lateral portion of the basicranium being entirely missing. In view of the differences in the construction of the basisphenoid and the parts of the auditory region present, however, it seems unlikely that the mastoid plates characteristic of *Apternodus* were present.

Mandible.—The horizontal ramus is slender with a straight alveolar border and a convexly curved lower margin so that the deepest part is below M_1. The coronoid process is triangular in shape and deflected laterally. The angle is slender and sharply inflected. The condyle is relatively short, oblique in position, and elevated considerably above the alveolar margin of the tooth row. The foramen mandibulare is just anterior to and slightly below the level of the condyle. In almost all features the mandible of *Oligoryctes* closely resembles that of *Microgale*. The exception is that the condyle in *Microgale* is transversely longer and more horizontal in position.

Relationships.—*Oligoryctes* is sharply set off from all of the described species of *Apternodus* by the small size, the presence of descending processes of the basisphenoid and the probable absence of the mastoid plates. The dentition is in many respects closely similar, especially to that of *Apternodus illifensis* Galbreath but differs in the large size of P^3, and the complete molarization of P^4.

In characters of the cheek teeth, and probably the anterior premolars and incisors, it most resembles the smaller Tenrecidae, particularly *Microgale*. The development of the basal internal cingulum of the molars is intermediate between *Oryzorictes*, in which the cingulum is produced into sharp, slender cusps, and *Microgale*, in which this cingulum is a low flaring heel. None of the Oryzorictinae have an enlarged P^3 or molarization of P^4, but these are characters of *Centetes*. There is nothing in the dentition, therefore, which would exclude *Oligoryctes* from the Tenrecidae.

The characters of the skull and mandible also as far as known are like the smaller Tenrecidae, although lacking the peculiar specializations of *Centetes*.

If the family Apternodontidae is revived, as is advocated in an earlier part of the paper, *Oligoryctes* would bear the same relationship to *Apternodus* as *Microgale* and *Oryzorictes* do to *Centetes* in the modern Tenrecidae. It is an adaptive variant in a radiation of this type of insectivore, which took place in North America in Eocene and Oligocene time. *Micropternodus* and *Clinopternodus* would be considered similar variants.

REFERENCES

BUTLER, P. M., 1937, Studies of the mammalian dentition I: the teeth of *Centetes ecaudatus* and its allies: Zool. Soc. London Proc., vol. 107, ser. B, p. 103–132.

CLARK, JOHN, 1937, The stratigraphy and paleontology of the Chadron formation in the Big Badlands of South Dakota: Carnegie Mus. Ann., vol. 25, p. 261–350.

DOBSON, G. E., 1882–1883, A monograph of the Insectivora, systematic and anatomical: London, John Van Voorst, pt. 1 (1882) p. 1–95; pt. 2 (1883) p. 97–172.

GALBREATH, E. C., 1951, A contribution to the Tertiary geology and paleontology of northeastern Colorado. Univ. Kansas Paleontological Pub., Vertebrata, art. 4, p. 1–120.

GREGORY, W. K., 1910, The orders of mammals: Am. Mus. Nat. Hist. Bull., vol. 27, p. 1–524.

MATTHEW, W. D., 1903, The fauna of the Titanotherium beds at Pipestone Springs, Montana: Amer. Mus. Nat. Hist. Bull., vol. 19, art. 6, p. 197–226.

——, 1910, On the skull of *Apternodus* and the skeleton of a new artiodactyl: Amer. Mus. Nat. Hist. Bull., vol. 28, art. 5, p. 35–42.

SCHLAIKJER, E. M., 1933, A detailed study of the structure and relationships of a new zalambodont insectivore from the middle Oligocene: Mus. Comp. Zool. Harvard Bull., vol. 76, p. 1–27.

——, 1934, A new fossil zalambodont insectivore. Am. Mus. Novitates, no. 698, p. 1–8.

SIMPSON, G. G., 1931, A new classification of mammals. Am. Mus. Nat. Hist. Bull., vol. 59, no. 1, p. 259–293.

——, 1945, The principles of classification and a classification of mammals: Am. Mus. Nat. Hist. Bull., vol. 85, p. 1–350.

WOOD, A. E., 1933, A new heteromyid rodent from the Oligocene of Montana: Jour. Mammalology, vol. 14, no. 2, p. 134–135.

WORTMAN, J. L., 1902, Studies of Eocene mammals in the Marsh collection: Am. Jour. Sci., vol. 13, p. 93–98.

MANUSCRIPT RECEIVED AUGUST 3, 1955.

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 542–562, PL. 63–67, MAY 1956

UPPER CAMBRIAN TRILOBITES FROM WESTERN WYOMING

CHARLES R. DELAND AND ALAN B. SHAW
Stanolind Oil and Gas Co., Albuquerque, and Shell Oil Co., Denver

ABSTRACT—The Upper Cambrian trilobites from three measured sections in the Gros Ventre and Wind River Mountains, Wyoming, are described. Collections include 22 named species and 26 named genera, of which 22 forms are new to Wyoming. Representatives of the *Cedaria, Crepicephalus, Elvina, Conaspis* and *Ptychaspis-Prosaukia* zones are present as well as two cranidia probably assignable to the Trempealeauan stage.

New species described are *Apachia convexa, Dellea saginata, Iddingsia occidentalis* and *Meteoraspis boulderensis.*

INTRODUCTION

THIS article is based upon part of a thesis submitted in September 1954, by the senior author to the Department of Geology and the Graduate School of the University of Wyoming in partial fulfillment of the requirements for the degree of Master of Arts. The full details of the stratigraphy will be published separately by the senior author, although columnar sections based on this work and a statement of the stratigraphic nomenclature involved have already been published (Shaw & DeLand, 1955). The junior author, who revised and edited the original manuscript for publication wishes to acknowledge the assistance of a grant-in-aid from the Graduate Research Council, University of Wyoming, under which the photographs on the accompanying plates were printed and the final manuscript typed by Mrs. G. C. Hertzfeldt.

STRATIGRAPHIC SUMMARY

Although the stratigraphic terminology used herein has been published, the publication is probably not accessible to many readers, so it is reviewed here; it is also summarized in Table 1. Basically, the old Gallatin and Gros Ventre "formations" have been raised to the rank of groups, and the readily mappable units that were formerly classed as members have been raised to the rank of formations. Where local names are available they have been used, but the names Park shale and Wolsey shale have been imported from Montana and northwestern Wyoming, and the name Open Door limestone (new in Shaw & DeLand, 1955) is applied to the top of the old Gallatin.

Gallatin group.—The elevation of the old "Gallatin formation" to the status of a group was first suggested by Deiss (1936, p. 1340–1341; 1938, p. 1103–1104) and has been formally proposed by Shaw (1954a). The recognition of the Gallatin as a group allows the continued use of the name for the entire upper carbonate sequence in western Wyoming, in the sense that is is now current and at the same time permits recognition

TABLE 1.—STRATIGRAPHIC NOMENCLATURE FOR THE CAMBRIAN OF WESTERN WYOMING

Gros Ventre Mountains and northern and central Wind River Mountains	Southern Wind River Mountains
Gallatin group	Gallatin group
Open Door limestone	Open Door limestone
Dry Creek shale member	Dry Creek shale member
DuNoir limestone	DuNoir limestone
Gros Ventre group	Gros Ventre formation
Park shale	
Death Canyon limestone	
Wolsey shale	
Flathead sandstone	Flathead sandstone

of the mappable formations within the Gallatin where that is deemed desirable.

Open Door limestone.—The name "Open Door limestone" has been proposed (Shaw & DeLand, 1955) for the carbonate sequence formerly known as the "Upper Gallatin limestone." The type section lies below the pillar of Bighorn dolomite known as "The Open Door" in Granite Canyon, SW¼, sec. 5, T. 39 N., R. 113 W., Teton Co., Wyoming. The name is used to include the Dry Creek shale member and all rocks above it to the top of the Gallatin group, regardless of age. Names previously applied to these rocks or to parts of them have required a knowledge of the fauna before the proper name could be applied; names so based are here rejected as unworkable for the practical field geologist.

Dry Creek shale member.—Lochman (1950) thoroughly discussed the Dry Creek shale, which forms the basal member of the Open Door limestone wherever the DuNoir limestone lies below it to separate it from the Park shale or the Gros Ventre formation.

DuNoir limestone.—The DuNoir limestone is ubiquitous in western Wyoming, the name for it having been introduced by Miller (1936, p. 125) in the northeastern Wind River Mountains.

Gros Ventre group.—The Gros Ventre "formation" of most authors is here regarded as a group in those areas where the Death Canyon limestone is present and as a formation where the disappearance of the Death Canyon leaves an unbroken clastic sequence between the Flathead sandstone and the Gallatin group, as at Sweetwater Canyon.

Park shale.—The name Park shale (Montana) is here applied to the shaly unit previously called the "upper shale member of the Gros Ventre formation." The Middle-Upper Cambrian boundary lies in the upper part of the Park shale in most sections in Wyoming.

Death Canyon limestone.—The Death Canyon limestone, named by Miller (1936, p. 119–120) as a member of the Gros Ventre formation is here regarded as a formation in the Gros Ventre group.

Wolsey shale.—The name Wolsey shale is brought down from Montana and applied to its equivalents, the "lower Gros Ventre shale."

These nomenclatural changes have been outlined by DeLand (1954), Shaw (1954b) and Shaw & DeLand (1955) as applicable widely in Wyoming; further detailed discussion of them will be presented elsewhere.

THE SECTIONS

During the Summer of 1953 the senior author measured and collected the Cambrian sequence at Granite Falls, Gros Ventre Range, at Steele Butte, west of the main mass of the Wind River Mountains, and at Sweetwater Canyon in the southern Wind River Mountains. A detailed list of localities is appended below. Although the entire Cambrian section was measured and sampled at each place, time did not permit the study of the Middle Cambrian collections; these will be described at a later date. Preliminary fossil lists have been given by Shaw & DeLand (1955).

Locality Register

The numbering system used at the University of Wyoming for fossil localities in Wyoming is fractional, with the numerator formed of the township and range in which the collection was made. The denominator contains the section number, a letter designating the specific collection, and a number indicating stratigraphic position. Thus, collections from Granite Falls, made in SW¼, sec. 5, T. 39 N., R. 113 W., Teton Co., have the general number 39113/5A, with the individual samples ranging from 39113/5A1, at 25.3 feet above the base of the Park shale to 39113/5A6 at 13.8 feet above the base of the Open Door limestone. Middle Cambrian collections are not listed.

Granite Falls.—Location given above.

39113/5A6— 13.8 feet above the base of the Open Door limestone
Camaraspis plana Frederickson
Elvinia sp. indet.

39113/5A5— 12.7 feet above the base of the Open Door limestone
Elvinia sp. indet.

Steele Butte.—Collections were made near the north end of the hill called Steele Butte, southeast of Boulder, in SW¼, sec. 20, T. 32 N., R. 107 W., Sublette County. The general locality number is 32107/20B. Individual collections are:

32107/20B25—33.0–33.6 feet above the base of the Open Door limestone

Camaraspis plana
Elvinia sp. indet.

32107/20B24—25–30 feet above the base of the Open Door limestone
Burnetia alta
Camaraspis plana
Dellea cf. *D. butlerensis*
D. suada?
Elvinia sp. indet.

32107/20B23—8–9 feet below the top of the Du-Noir limestone
Coosia dakotensis
Coosia connata?

32107/20B22—2.2–2.7 feet below the top of the Park shale
Arapahoia butleri
Blountia carlotta
Cedaria milleri
Meteoraspis elongata
Bynumia sp. indet.
Modocia sp. indet.

32107/20B20—10.5–10.6 feet below the top of the Park shale
Modocia centralis
Arapahoia sp. indet.
"*Cedarina*" sp. indet.
Leiocoryphe sp. indet.
Meteoraspis sp. indet.

32107/20B19—20.4–20.6 feet below the top of the Park shale
Arapahoia levis
Blountia carlotta
Meteoraspis boulderensis
Kingstonia sp. indet.

32107/20B15—44.0–44.4 feet below the top of the Park shale
Kingstonia spicata
Kormagnostus sp. indet.
Cranidium A.

32107/20B14—47.8–48.2 feet below the top of the Park shale
Kingstonia spicata
Pygidium A.

Sweetwater Canyon.—Two collections were made in Sweetwater Canyon. The first was from SW¼, sec. 27, T. 29 N., R. 97 W., Fremont County, and is designated 2997/27A. The second, from NE¼, sec. 34, is designated 2997/34A. Individual collections from the former are:

2997/27A14—184.0–185.0 feet above the base of the Open Door limestone
Cranidium B
Cranidium C

2997/27A12—83.5–84.0 feet above the base of the Open Door limestone
Idahoia sp. indet.
Monocheilus? sp. indet.

2997/27A11—53.0–54.0 feet above the base of the Open Door limestone
Taenicephalus cordillerensis

2997/27A10—1.0–1.5 feet above the base of the Open Door limestone
Apachia convexa
Burnetia
Cliffia latagenae
Deadwoodia duris
Dellea saginata
Housia vacuna?

Explanation of Plate 63

All specimens on this plate from the *Cedaria* zone of the upper Park shale at Steele Butte (Loc. 32107/20B).

Fig. *1*—*Arapahoia butleri* (Stoyanow), 1936. Cranidium. Length 20.0 mm. UW A10904a. Loc. 32107/20B22. (p. 546)

2—*Arapahoia* sp. indet. Immature cranidium. Length 3.1 mm. UW A10899. Loc. 32107/20B20. (p. 547)

3–8—*Blountia carlotta* Lochman, 1944. *3,4*, Smooth cranidium provisionally assigned to species. UW A10902c. Length 8.1 mm. Loc. 32107/20B19. *5*, Small cranidium. Length 5.2 mm. UW A10894. *6,7*, Larger, more typical cranidium. Length of glabella 7.0 mm. UW A10902d. *8*, Assigned pygidium. Maximum length 3.6 mm. UW A10902a. Fig. 5–8 from Loc. 32107/20B22. (p. 548)

9–11—*Bynumia* sp. indet. Dorsal, anterior and lateral views of cranidium. Length of cranidium 9.5 mm. UW A10900b. Loc. 32107/20B22. (p. 549)

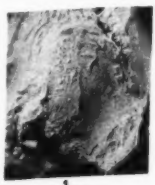
12—*Arapahoia levis* Miller, 1936. Cranidium. Length 10.9 mm. UW A10895. Loc. 32107/20B19. (p. 547)

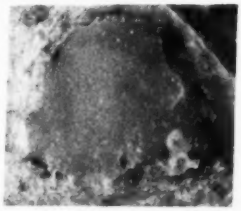
13–15—*Cedaria milleri* Resser, 1937. *13,14*, Largest cranidium. Length 2.5 mm. UW A10930a. *15*, Smaller cranidial fragment preserving posterior limb. Length of glabella 3.2 mm. UW A10930b. Both specimens from Loc. 32107/20B22. (p. 549)

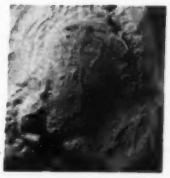
16—*Kingstonia* sp. indet. Unassigned pygidium. Length 2.3 mm. UW A10892. Loc. 32107/20B19. (p. 557)

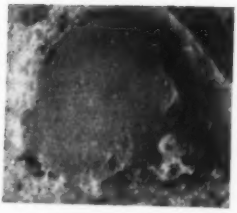
17—*Kingstonia spicata* Lochman, 1940. Best preserved pygidium. Maximum width 4.8 mm. UW A10888a. Loc. 32107/20B15. (p. 556)

18—*Meteoraspis boulderensis* DeLand, n. sp. Dorsal view of holotype cranidium (See Pl. 64, fig. 4,5.) Length 11.1 mm. UW A10891a. Loc. 32107/20B19. (p. 557)


1

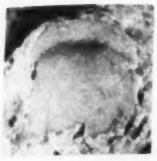

2

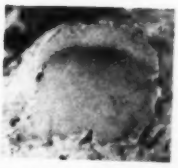




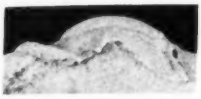
3

6

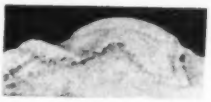

4

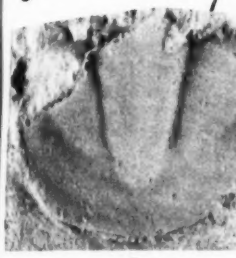


5


7

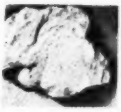
9

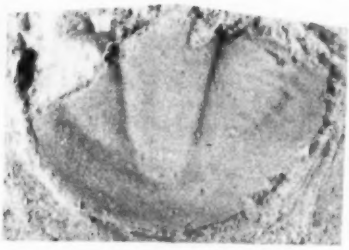


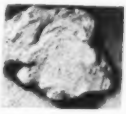

8

10

11

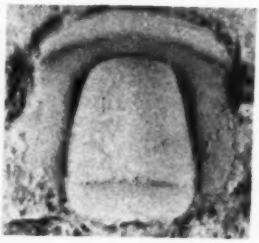

12

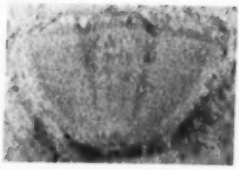




13

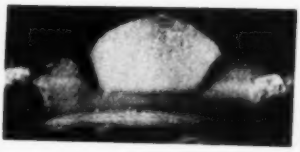
16





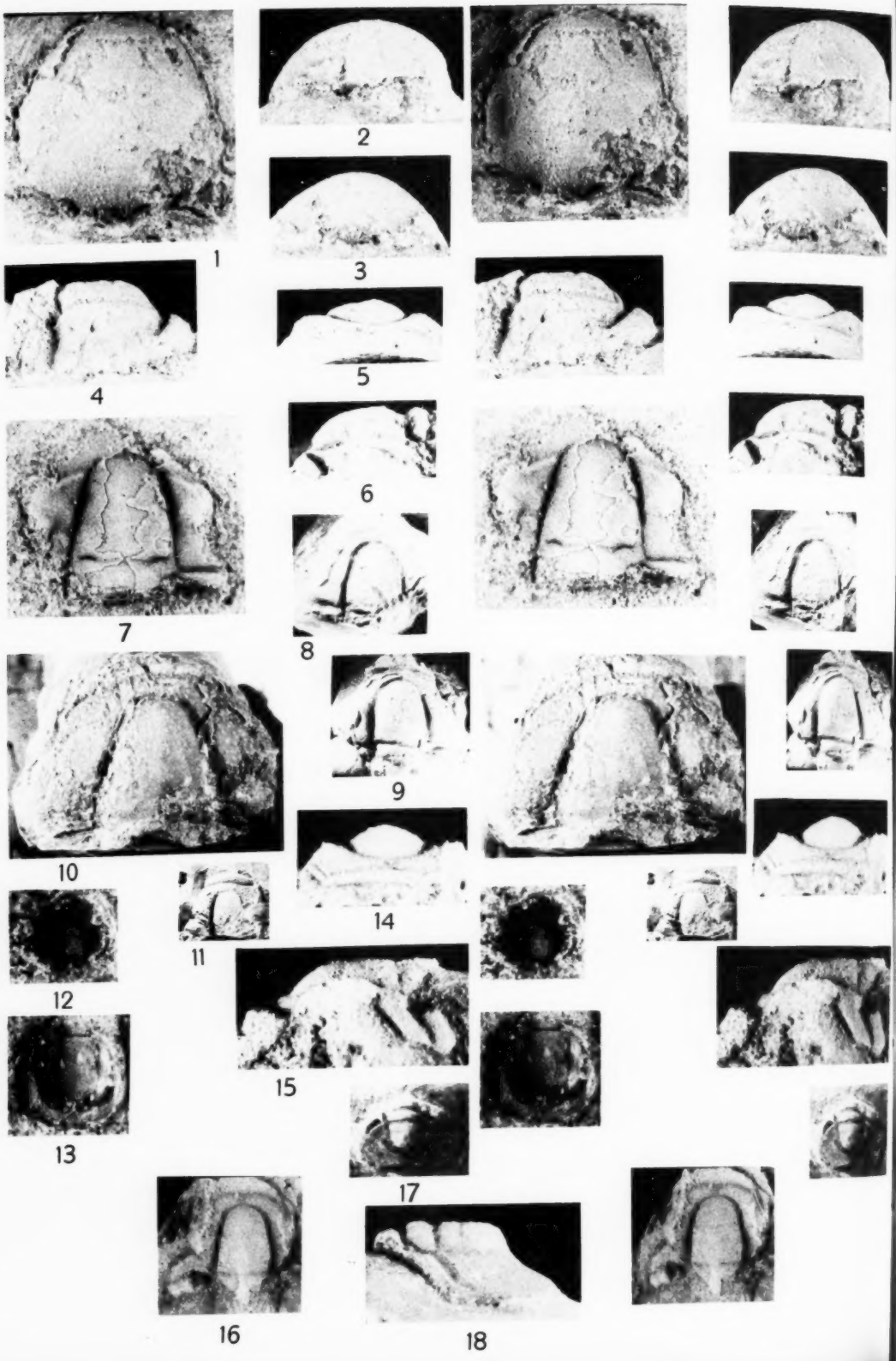
14

17



15

18


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

Iddingsia occidentalis
Irvingella aff. *I. flohri*
Xenocheilos cf. *X. spineum*
Elvinia sp. indet.

Individual collections from the latter are:

2997/34A2— 131.6–131.7 feet above the base of the Open Door limestone
Ellipsocephaloides sp. indet.

2997/34A1— 80.3–80.7 feet above the base of the Open Door limestone
Taenicephalus cordillerensis

FAUNAL SUMMARY

Five of the standard Upper Cambrian faunal zones have been recognized in the collections described here: the *Cedaria*, *Crepicephalus*, *Elvinia*, *Conaspis* and *Ptychaspis-Prosaukia* zones. In addition, two unidentified cranidia from Trempealeauan equivalents have not yet been assigned to any zone. Lists of forms identified in each zone follow:

Cedaria zone:
Arapahoia butleri
A. levis
A. sp. indet.
Blountia carlotta
Bynumia sp. indet.
Cedaria milleri
"*Cedarina*" sp. indet.
Kingstonia spicata
K. sp. indet.
Kormagnostus sp. indet.
Leiocoryphe sp. indet.
Meteoraspis boulderensis
M. elongata
M. sp. indet.
Modocia centralis
M. sp. indet.
Cranidium A
Pygidium A

Crepicephalus zone:
Coosia connata?
C. dakotensis

Elvinia zone:
Apachia convexa
Burnetia alta
Camaraspis plana
Cliffia latagenae
Deadwoodia duris
Dellea cf. *D. butlerensis*
D. saginata
D. suada?
Elvinia sp. indet.
Housia vacuna?
Iddingsia occidentalis
Irvingella aff. *I. flohri*
Xenocheilos cf. *X. spineum*

Conaspis zone:
Taenicephalus cordillerensis

Trempealeauan (zone unknown):
Cranidium B
Cranidium C

EXPLANATION OF PLATE 64

All specimens from the *Cedaria* zone of the upper Park shale at Steele Butte (Loc. 32107/20B).

FIG. *1–3*—*Leiocoryphe* sp. indet. Dorsal, lateral and anterior views of cranidium. Length of cranidium 3.9 mm. UW A10897. Loc. 32107/20B20. (p. 557)

4–6—*Meteoraspis boulderensis* DeLand, n. sp. *4,5*, Lateral and anterior views of holotype cranidium (see Pl. 63, fig. 18). UW A10891a. *6*, Lateral view of paratype cranidium, showing undamaged profile. Length 10.9 mm. UW A10891b. Loc. 32107/20B19. (p. 557)

7—Cranidium A. Dorsal view of unidentified cranidium. Length of glabella 4.4 mm. UW A10889. Loc. 32107/20B15. (p. 552)

8—*Meteoraspis* sp. indet. Cranidium ×1. UW A10898. Loc. 32107/20B20. (p. 558)

9—*Meteoraspis elongata* Lochman, 1944. Cranidium. Length 17.6 mm. UW A10903. Loc. 32107/20B22. (p. 558)

10—*Modocia centralis* (Whitfield), 1877. Cranidium. Length 14.7 mm. UW A10896a. Loc. 32107/20B20. (p. 558)

11—*Modocia* sp. indet. Fragmentary cranidium ×1. UW A10901. Loc. 32107/20B22. (p. 559)

12–13—*Kormagnostus* sp. indet. Fragmentary cephalon and pygidium. Length of posterior glabellar segment 0.8 mm. Length of pygidium 2.0 mm. UW A10890b,c. Loc. 32107/20B15. (p. 557)

14–16—"*Cedarina*" sp. indet. Anterior, lateral and dorsal views of unique cranidium. Length of glabella, excluding occipital ring 2.2 mm. UW A10936. Loc. 32107/20B20. (p. 550)

17–18—Pygidium A. Dorsal and lateral views. Length 8.0 mm. UW A10886. Loc. 32107/10B14. (p. 561)

DESCRIPTION OF SPECIES

Genus APACHIA Frederickson, 1949

APACHIA CONVEXA DeLand, n. sp.

Pl. 65, fig. 4–6

Description.—Cranidium quadrate, highly convex. Glabella very highly convex, conical, smoothly rounded anteriorly, no glabellar furrows. In longitudinal profile, the greatest convexity of the glabella is immediately anterior to the occipital furrow. In transverse profile, the gently convex sides of the glabella rise steeply from the dorsal furrow to the smoothly rounded crest. Occipital furrow broad and deep at the axis of the cranidium, shallower near dorsal furrow. Occipital ring broad, somewhat flattened, untapered. Dorsal furrow broad and deep at sides of glabella, less deeply impressed anteriorly. Brim convex, posterior part forming a narrow, downsloping platform which merges laterally with fixed cheeks; anterior rolled sharply down to a nearly vertical position at the marginal furrow, which is wide, deep and gently curved. Border convex, about same length as brim, nearly horizontal at marginal furrow. Fixed cheeks about one-half as wide as glabella, regularly convex in all directions. Palpebral lobe about one-third the length of the glabella, narrow, gently curved, depressed, centered slightly forward of the center of the glabella. Palpebral furrow faint, nearly straight. No ocular ridge. Posterior limb triangular, convex, steeply depressed laterally, marginal furrow wide and deep at lateral extremity, shallow at junction with dorsal furrow.

Facial suture cuts anterior margin on a line with the dorsal furrow, curves gently out and back to marginal furrow, trends nearly straight back and slightly inward to anterior end of palpebral lobe, curves gently around the lobe, indents slightly, and then curves out and back on an increasingly convex course to cut the posterior margin within the genal angle.

Outer surface of test very finely granulated.

Free cheeks, thorax and pygidium unknown.

Remarks.—The holotype is a single, nearly complete cranidium, 3.2 mm. long and 3.4 mm. wide. In addition to its slightly smaller size it differs from *A. trigonis* in the following respects:

Feature	*Apachia trigonis*	*Apachia convexa*
Occipital ring	Convex	Flattened
Brim	Gently convex. Descends from dorsal furrow at nearly same angle as front of glabella.	Strongly convex. Posterior portion forms downsloping platform, anterior portion nearly vertical.
Border	Rises at 45° angle from marginal furrow.	Nearly horizontal at marginal furrow.
Fixed cheeks	Flat in transverse profile.	Convex in transverse profile.

Locality and formation.—Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Figured specimen.—UW A10924a.

Genus ARAPAHOIA Miller, 1936

ARAPAHOIA BUTLERI (Stoyanow), 1936

Pl. 63, fig. 1

Hesperaspis butleri STOYANOW, 1936, Geol. Soc. Am. Bull., vol. 47, p. 469, pl. 1, fig. 8.

Arapahoia butleri (Stoyanow). RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 2.

Arapahoia reesidei RESSER, 1942, Smithsonian Misc. Col., vol. 103, no. 5, p. 44–45, pl. 7, fig. 5–9.

Diagnosis.—*Arapahoia* with stubby posterior limbs, eyes noticeably removed from the dorsal furrow, and the glabella faintly outlined, even on the exterior of the test.

Description.—Cranidium spatulate, convex in both directions. Glabella conical, bluntly rounded in front. Broad shallow concavities opposite the eyes and in the posterior quarter of the glabella may be glabellar furrows, but they are poorly defined. Glabella evenly convex longitudinally and transversely; little change in convexity

across the dorsal furrows to the rest of the cranidium. Occipital furrow broad, shallow, deflected anteriorly in the middle; furrow not well marked on either inside or outside of test. Occipital ring broad, triangular, nearly flat in longitudinal profile, and apparently equipped with a slender spine. Dorsal furrow faint all around. Brim flatly convex, downsloping nearly in the same curve as the glabellar profile, smooth. Fixed cheeks one-third to one-quarter as wide as glabella, opposite the eyes. Palpebral lobes nearly horizontal, gently arched longitudinally, one-third as long as the glabella excluding the occipital ring, centered about opposite the middle of the cranidium, excluding the occipital spine. No ocular ridge. Posterior limbs less wide than usual for the genus, being slightly over half as wide as the occiptal ring. Marginal furrow well defined. Facial suture trends slightly outward in front of the eyes and bows outward in a regular curve behind.

Surface and inside of test smooth.

Free cheeks, thorax and pygidium not collected, but figured by Resser (1942, pl. 7, fig. 5).

Remarks.—This species is very close to *Arapahoia convexa* Duncan, 1944 (=*A. polita* and *A. prolixa* Resser, 1942) in the stubby posterior limbs and in the configuration of the eyes, but it differs in having dorsal furrows. Probably the difference is no more than subspecific.

There seem to be two divisions of the genus *Arapahoia*, one, with eyes set close to the glabella and virtually rising from the dorsal furrow as in *A. spatulata* Miller, 1936, and the other, with eyes separated from the furrow by one-fifth to one-third of the glabellar width, as in *A. typa*. These two divisions may, on further study, warrant subgeneric separation.

This is the largest *Arapahoia* thus far found in Wyoming.

Locality and formation.—Two cranidia from the Steele Butte collection 32107/20B22, 2.7–4.2 feet below the top of the Park shale. *Cedaria* zone.

Plesiotypes.—UW A10904.

ARAPAHOIA LEVIS Miller, 1936
Pl. 63, fig. 12

Arapahoia levis MILLER, 1936, Jour. Paleont., vol. 10, p. 25, pl. 8, fig. 3,4.

Description.—Cranidium nearly smooth, flat. Glabella undifferentiated on outer surface, slightly longer than wide, low and flat, scarcely elevated above fixed cheeks, no glabellar furrows. Occipital furrow wide and shallow, nearly obsolete at axis, directed backward laterally. Occipital ring narrower than base of glabella, flat, tapers posteriorly into a broad spine of unknown length. Dorsal furrow obsolete on outer surface, narrow and shallow but complete on exfoliated specimens. Preglabellar area one-third as long as glabella, undifferentiated on outer surface. On exfoliated specimens a faint, narrow marginal furrow divides the preglabellar area subequally into a convex, arcuate border and a nearly flat brim. Fixed cheeks flat, horizontal, less than one-half as wide as glabella. Palpebral lobes of medium length, crescentiform, slightly elevated, situated opposite anterior third of the glabella. Palpebral furrow obsolete. No ocular ridge. Posterior limbs triangular, moderately depressed, about one-half as wide as base of glabella; marginal furrow wide and deeper than any of the other cranidial furrows.

Anterior course of facial suture broadly curved in front, then directed nearly straight back to front of palpebral lobe, curving widely around and indented behind palpebral lobe; directed out and back at an angle of about 45° and then abruptly back to cut posterior margin.

Free cheeks, thorax and pygidium unknown.

Remarks.—*Arapahoia levis* differs from *A. typa* in the rounded anterior margin of the cranidium and the smoother surface. It differs from *A. butleri* in its smaller size, wider posterior limbs, rounded anterior margin and in its effacement.

Locality and formation.—Three fragmentary cranidia and one complete, but weathered, exfoliated cranidium from Steele Butte collection 32107/20B19, 20.4–20.6 feet below the top of the Park shale. *Cedaria* zone.

Plesiotypes.—UW A10893, A10895.

ARAPAHOIA sp. indet.
Pl. 63, fig. 2

Description.—Cranidium smooth, length two-thirds the width across posterior limbs, in longitudinal profile regularly and gently

convex. Glabella flatly keeled, not differentiated from brim and fixed cheeks, faintly demarcated from posterior limbs by shallow, incomplete dorsal furrow. Occipital furrow wide and shallow. Occipital ring wide, flat, apparently unspined. Brim and border undifferentiated, flat; preglabellar area continues the anterior slope of the glabella. Fixed cheeks flat, downsloping, continuing the lateral slope of the glabella. Palpebral lobes large, curved, raised very slightly above the fixed cheeks, situated opposite anterior end of glabella. Posterior limbs triangular, slightly longer than wide, flat, downsloping. The marginal furrow is broad and more deeply impressed than the occipital furrow.

Anterior facial suture broadly rounded across the front of the cranidium then directed straight back to anterior end of palpebral lobe; curves around and is indented at posterior end of palpebral lobe, thence nearly straight and directed at an angle of about 45° with the axis to cut the posterior margin.

Surface covered with faint, fine granules arranged in irregular longitudinal lines except on the border where the lines are transverse.

Remarks.—This specimen is immature, and it is impossible to assign it to a species with certainty, but it is possible that it may be a young *A. levis*; the smooth surface suggests this.

Locality and formation.—Steele Butte collection 32107/20B20, 10.5–10.6 feet below the top of the Park shale. *Cedaria* zone.

Figured specimen.—UW A10899.

Genus BLOUNTIA Walcott, 1916
BLOUNTIA CARLOTTA Lochman, 1944
Pl. 63, fig. 3–8

Blountia carlotta LOCHMAN, 1944, in Lochman & Duncan, Geol. Soc. Am. Spec. Pap. 54, p. 84–85, pl. 11, fig. 28–31.

There is nothing to add to the full description of this species given by Lochman.

Remarks.—Specimens identified with this species have been found at two levels in the Park shale (see below). Most of the specimens (Pl. 63, fig. 5–7) seem to be typical of the species, but one of the younger specimens (Pl. 63, fig. 3,4) is smoother and has a narrower marginal furrow. These differences do not now seem sufficient to warrant exclusion of the cranidium from the species.

Locality and formation.—Steele Butte collections 32107/20B19 (one cranidium) and 32107/20B22 (2 cranidia, 1 pygidium), 20.4–20.6 and 2.7–4.2 feet below the top of the Park shale, respectively. *Cedaria* zone.

Plesiotypes.—UW A10894, A10902a–d.

Genus BURNETIA Walcott, 1924
BURNETIA ALTA Resser, 1942
Pl. 65, fig. 1–3

Burnetia alta RESSER, 1942, Smithsonian Misc. Coll., vol. 103, no. 5, p. 80–81, pl. 17, fig. 12–14.

Burnetia alta Resser. WILSON, 1951, Jour. Paleont., vol. 25, p. 626.

Description.—Cranidium elongate, moderately to highly convex. Glabella highly convex in holotype, less so in Wyoming specimens; sides gently tapered, slightly curved; anterior rounded. Two pairs of glabellar furrows; anterior pair reduced to short notches; posterior pair longer, curved backward, deep on internal molds and on young individuals, shallow on the exterior of larger cranidia. Occipital furrow narrow but well defined, nearly straight across the middle half of the glabella, then swinging forward on both ends. Occipital ring of nearly uniform width throughout; no spine present. Dorsal furrows impressed all around glabella, but not deep; faint anteriorly, deeper laterally. Brim reduced medially to a strip scarcely a millimeter wide between the dorsal and marginal furrows. Marginal furrow well defined, curved and nearly tangent to dorsal furrow at center, directed nearly straight and obliquely back laterally. Border flat and downsloping, about one-third the length of glabella, anterior broadly rounded. Fixed cheeks transversely convex, upsloping from dorsal furrow, downsloping at lateral margin, about one-third as wide as glabella; ocular ridge strong and oblique. Palpebral lobes and posterior limbs unknown.

Free cheek broadly rectangular. Ocular platform regularly convex. Marginal furrow wide and well impressed, posterior marginal furrow most deeply impressed. Border about one-half as wide as ocular platform, smoothly concave, extended posteriorly into a long, sharp spine.

Facial suture describes smooth curve about antero-lateral corner of cranidium and converges slightly from opposite marginal furrow toward palpebral lobe. Further course unknown.

Outer surface irregularly covered with coarse pustules which are smaller and fewer on border than on rest of cranidium. Ocular platform also pustulose.

Pygidium semicircular, length about one-half width. Axis extends nearly full length of pygidium, highly convex, tapered; four axial rings and a posterior segment separated by distinct furrows. Dorsal furrow narrow and well impressed. Pleural platform moderately convex with an abrupt deflection down to the concave border. Border and pleural platform about equal in width at sides of pygidium. Pleural lobes marked by four segments which bend back slightly at marginal furrow and extend across border. Interpleural grooves distinct; pleural furrows wider and deeper than interpleural grooves on anterior three segments. Marginal furrow shallow.

Remarks.—This species differs from *B. urania*, as Wilson has pointed out, in the shortness of the border.

Locality and formation.—Steele Butte collection 32107/20B24, 25.0–30.0 feet above the base of the Open Door limestone (4 cranidia, 2 free cheeks, 1 pygidium). Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone (1 pygidium). *Elvinia* zone.

Plesiotypes.—UW A10908a,b, A10910a–c, A10911, A10926.

Genus BYNUMIA Walcott, 1924
BYNUMIA sp. indet.
Pl. 63, fig. 9–11

Description.—Cranidium broadly triangular, length about one-half width across posterior limbs, no furrows visible on outer surface of test, anterior bluntly pointed; posterior margin between posterior limbs gently convex. Cranidium is regularly convex in transverse profile except for faint flattening of the posterior limbs. In longitudinal profile, cranidium is nearly hemispherical with a slight increase in convexity near both anterior and posterior margins. Only posterior part of glabella well defined, even on exfoliated specimens. Dorsal furrow on the inside of the test broad and shallow at posterior margin, becomes more shallow and narrow anteriorly and is straight across the front end of the glabella. Occipital furrow marginal, broad and shallow, on interior of test only. Posterior limb approximately same width as glabella at occipital furrow, sharply triangular with a broad shallow marginal furrow present only on the inner surface. Fixed cheeks, brim and border undifferentiated. Palpebral lobes missing.

Outer surface of test microscopically granulated, inner surface finely punctate.

Remarks.—This species seems to differ from other described species in having a stubbier glabella and in being blunter anteriorly, but until more specimens are found it seems unwise to propose a new name.

Locality and formation.—Steele Butte collection 32107/20B22, 2.7–4.2 feet below the top of the Park shale (2 cranidia). *Cedaria* zone.

Plesiotypes.—UW A10900a,b.

Genus CAMARASPIS Ulrich & Resser, 1924
CAMARASPIS PLANA Frederickson, 1948
Pl. 66, fig. 13

Camaraspis plana FREDERICKSON, 1948, Jour. Paleont., vol. 22, p. 799, pl. 123, fig. 14–15.

The Wyoming specimens add nothing to Frederickson's original description.

Remarks.—The bifurcation of the occipital furrow, mentioned by Frederickson, was observed faintly or not at all on the Wyoming specimens, all of which are exfoliated cranidia, but lateral widening of the occipital furrow may indicate the position at which the occipital furrow bifurcates on the outer surface of the test.

Location and formation.—Granite Falls collection 39113/5A6, 13.8 feet above the base of the Open Door limestone. Steele Butte collections 32107/20B24 and 32107/20B25, 25.0–30.0 and 33.0–33.6 feet above the base of the Open Door limestone, respectively. *Elvinia* zone.

Plesiotypes.—UW A10908a,b, A10909a–d, A10911, A10914, A10917.

Genus CEDARIA Walcott, 1924
CEDARIA MILLERI Resser, 1937
Pl. 63, fig. 13–15

Cedaria aff. *C. prolifica* Walcott. MILLER, 1936, Jour. Paleont., vol. 10, p. 28–29, pl. 8, fig. 18.

Cedaria milleri RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 5.

Description.—Cranidium, excluding the posterior limbs, quadrate, longer than wide. Glabella conical, moderately and regularly convex, anterior smoothly rounded, length about equal to width, no glabellar furrows. Occipital furrow of medium width, well impressed except at junction with dorsal furrow. Occipital ring wide at center, tapered laterally, flat, with a median node. Dorsal furrow narrow, sharply but not deeply impressed. Preglabellar area about two-fifths as long as glabella, sub-equally divided into a nearly straight, gently downsloping brim and a flattened-convex, tapered border by the wide, shallow, gently curved marginal furrow. Fixed cheeks slightly convex and gently downsloping, a little more than one-half as wide as glabella. Palpebral lobes small, crescentic, slightly elevated above fixed cheeks, situated slightly anterior to glabellar mid-line. Palpebral furrow of medium width, shallow. Ocular ridge prominent, broadly curved from anterior end of palpebral lobe to antero-lateral corner of glabella. Posterior limbs strap-like, nearly as wide as occipital ring, laterally depressed, wider at lateral extremity than at junction with fixed cheek, posterior margin directed gently backward; marginal furrow wide and well-impressed, becoming more shallow and curving forward at outer end.

Facial suture cuts anterior margin slightly inside a line extended forward from the eyes, curves smoothly back to marginal furrow, converges noticeably toward the anterior end of the eye, swings around and indents behind the palpebral lobe, then runs outward nearly normal to axis of cranidium, curving abruptly backward to truncate the outer end of the posterior limb and cut the posterior margin within the genal angle.

Outer surface covered with small but distinct granules.

Free cheeks, thorax and pygidium unknown.

Remarks.—The two small, fragmentary cranidia are well preserved in limestone and add to the understanding of the species which previously was known only from the holotype. Apparently this species is rather restricted geographically. It was first collected by Miller near DuNoir, Wyoming, about 65 miles from where these two specimens were collected at Steele Butte.

Locality and formation.—Steele Butte collection 32107/20B22, 2.7–4.2 feet below the top of the Park shale. *Cedaria* zone.

Figured specimens.—UW A10930a,b.

Genus CEDARINA Lochman, 1940

"CEDARINA" sp. indet.

Pl. 64, fig. 14–16

Description.—Cranidium elongate, moderately convex. Glabella conical, tapered, angular in transverse profile, smoothly convex in longitudinal profile; two pairs of straight glabellar furrows are faintly indicated; anterior smoothly rounded. Occipital furrow shallow at axis, more deeply impressed at sides. Occipital ring flat and tapered, prolonged into a slender, flat-lying spine. Dorsal furrow complete, wide and shallow around anterior end of glabella, deeper along sides of glabella. Preglabellar area two-fifths as long as glabella; brim gently convex and downsloping except for a narrow axial groove on the mid-line of the brim. Border slightly convex, horizontal, arcuate, almost twice as long at center as brim. Marginal furrow wide and prominent, broadly curved with a slight posterior inbend opposite the axial groove. Fixed cheeks a little more than one-third as wide as glabella, nearly flat and considerably upsloping from dorsal furrow. Palpebral lobe of medium length, gently bowed, situated on median line of glabella and above the fixed cheek; palpebral furrow faint. Ocular ridge broad and low, curved from anterior end of palpebral lobe to the antero-lateral corner of the glabella. Posterior limb strap-like, as wide or wider than occipital ring, posterior margin directed obliquely backward; marginal furrow wide and deep.

Facial suture intramarginal nearly to center, curved smoothly out and back to marginal furrow, apparently directed straight back to palpebral lobe about which it curves and indents at the posterior end. Directed outward nearly parallel to posterior margin then swings abruptly back to cut the posterior margin.

Outer surface of test minutely granulated.

Free cheeks, thorax and pygidium unknown.

Remarks.—This species, known from a

single cranidium, probably represents a new genus and is placed in *Cedarina* only for convenience. Its distinctive features include the oblique, rearward direction of the posterior margin, the axial groove in the brim, and the elevated, close-set eyes. However, one specimen is not sufficient basis upon which to erect a new genus.

Locality and formation.—Steele Butte collection 32107/20B20, 10.5–10.6 feet below the top of the Park shale. *Cedaria* zone.

Figured specimen.—UW A10936.

Genus CLIFFIA Wilson, 1951
CLIFFIA LATAGENAE (Wilson), 1949
Pl. 65, fig. 11–12

Acrocephalites latagenae WILSON, 1949, Jour. Paleont., vol. 23, pl. 31, pl. 10, fig. 14.
Cliffia latagenae (Wilson). WILSON 1951, Jour. Paleont., vol. 25, p. 633, pl. 90, fig. 18–24.

The Wyoming specimens add nothing to Wilson's original description.

This species is represented in the collections by a nearly complete pygidium and a fragmentary cranidium on the same block of limestone with *Apachia convexa* DeLand and *Xenocheilos* cf. *X. spineum* Wilson, 1951. The pygidium is 1.3 mm. long with seven axial rings and a posterior segment. The axial lobe is nearer one-third the width of the pygidium than one-fourth which may be a function of the small size of the specimen. The cranidium is too fragmentary to add anything to the description of the species.

Locality and formation.—Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Figured specimens.—UW A10924b,c.

Genus COOSIA Walcott, 1911
COOSIA CONNATA (Walcott), 1890?
Pl. 67, fig. 6

Ptychoparia connata WALCOTT, 1890, U. S. Nat. Mus. Proc., vol. 13, p. 272, pl. 21, fig. 2.
Coosia connata (Walcott). RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 7.
Coosia connata (Walcott). LOCHMAN & DUNCAN, 1944, Geol. Soc. Am. Spec. Pap. 54, p. 46, pl. 6, fig. 7,8.

Remarks.—One fragmentary cranidium is tentatively referred to this species. In all of the preserved features it appears to be identical to previously illustrated specimens, but because of the fragmentary condition, the specific identification is questioned.

Locality and formation.—Steele Butte collection 32107/20B23, 8.0–9.0 feet below the top of the DuNoir limestone. *Crepicephalus* zone.

Plesiotype.—UW A10906.

COOSIA DAKOTENSIS Resser, 1942
Pl. 67, fig. 5

Coosia dakotensis RESSER, 1942, Smithsonian Misc. Coll., vol. 103, no. 5, p. 74, pl. 13, fig. 29–31.
Coosia grandis LOCHMAN in Lochman & Duncan, 1944, Geol. Soc. Am. Spec. Paper 54, p. 47–48, pl. 6, fig. 23–31.
Coosia dakotensis Resser. LOCHMAN & DUNCAN, 1949, Jour. Paleont., vol. 23, p. 439. Suppress *C. grandis* as a synonym.

The descriptions and figures by Lochman & Duncan and Resser fully characterize the species. The specimen from Steele Butte resembles the holotype in exhibiting a slight glabellar keel.

Locality and formation.—Steele Butte collection 32107/20B23, 8.0–9.0 feet below the top of the DuNoir limestone. *Crepicephalus* zone.

Figured specimen.—UW A10905.

Genus DEADWOODIA Resser, 1938
DEADWOODIA DURIS (Walcott), 1916
Pl. 65, fig. 7–10

Asaphiscus? duris WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 5, p. 392, pl. 63, fig. 8,8a.
Dunderbergia? declivita MILLER, 1936, Jour. Paleont., vol. 10, p. 30, pl. 8, fig. 37,38.
Deadwoodia duris (Walcott). WILSON, 1948, Jour. Paleont., vol. 22, p. 33, 34, pl. 8, fig. 9–17.

Remarks.—Wilson has restudied this species and given a full description of it.

This species was one of the most prominent members of the *Elvinia* fauna at Sweetwater Canyon where nine identifiable cranidia were collected. These cranidia differ from the holotype in possessing a slightly steeper brim, which may be a function of preservation.

Locality and formation.—Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Plesiotypes.—UW A10919a–i, A10928.

Genus DELLEA Wilson, 1949, emend. Wilson, 1951

DELLEA cf. D. BUTLERENSIS Frederickson, 1949

Pl. 66, fig. 1–3

Description.—Cranidium elongate, rectangular, moderately convex. Glabella conical, moderately convex, rounded anteriorly; two pairs of glabellar furrows visible on outer surface of test, anterior pair faint, short, oblique; posterior pair longer and bent sharply backward. Occipital furrow broad and bowed forward over axis; narrower, deeper and curved forward laterally. Occipital ring slightly convex. Dorsal furrow narrower than occipital furrow, well impressed, complete. Brim gently curved, continuing the slope of the anterior part of the glabella, slightly longer than the convex, arcuate border. Marginal furrow deep and broadly curved; radius of curvature about equal to length of cranidium. Fixed cheeks moderately convex, slightly more than one-third the width of the glabella; palpebral lobes one-fourth the length of the glabella, moderately curved, situated behind the glabellar median line and slightly below the dorsal furrow; palpebral furrow wide and shallow. Ocular ridge absent, but fixed cheek and border form rounded angle where ridge normally lies. Posterior limb short, triangular, slightly more than one-half as wide as the occipital ring; marginal furrow present but character is unknown.

Facial suture cuts anterior margin halfway between the axis and the corner of the cranidium, curves gently back to marginal furrow, converges slightly toward anterior end of palpebral lobe, swings out around lobe and then is directed nearly straight out at an angle of about 45° to cut the posterior margin.

Free cheeks, thorax and pygidium unknown.

Remarks.—Two fragmentary cranidia are similar to the *Dellea butlerensis* but differ in having an anterior axial flexure in the occipital furrow and in having a slightly narrower brim. Without more specimens the importance of these differences cannot be evaluated.

Locality and formation.—Steele Butte collection 32107/20B24, 25.0–30.0 feet above the base of the Open Door limestone. *Elvinia* zone.

Plesiotypes.—UW A10912a,b.

DELLEA SAGINATA DeLand, n. sp.

Pl. 66, fig. 4–7

Description.—Cranidium subquadrate, but damage to the antero-lateral angles make specimens appear subtriangular. Cranidium highly convex, length about two-thirds the

---

EXPLANATION OF PLATE 65

All specimens from the *Elvinia* zone of the Open Door limestone at Loc. 2997/27A10, except as noted.

FIG. *1–3—Burnetia alta* Resser, 1942. *1*, Damaged cranidium associated with cranidium of *Camaraspis plana* Frederickson, 1948 and pygidium of *Elvinia* sp. indet. Width of border at marginal furrow 18.7 mm. UW A10908a. *2*, Clay impression of assigned pygidium. ×1. UW A10926. *3*, Assigned free cheek. ×1. UW A10910a. *1* and *3* from Loc. 32107/20B24. (p. 548)

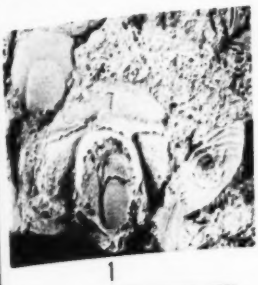
4–6—Apachia convexa DeLand n. sp. *4,6*, Dorsal and anterior views of holotype, associated with *Xenocheilos* cf. *X. spineum*. Length of cranidium 3.2 mm. *5*, Lateral view, lighted to demonstrate eccentric profile of glabella. UW A10924a. (p. 546)

7–10—Deadwoodia duris (Walcott), 1916. *7,10*, Anterior and dorsal views of cranidium. Length of glabella, excluding occipital ring, 5.8 mm. UW A10919a. *8,9*, Dorsal and lateral views of cracked cranidium preserving palpebral lobe and showing granular surface. Length of cranidium 9.5 mm. UW A10919b. (p. 551)

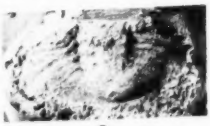
11,12—Cliffia latagenae Wilson, 1949. Cranidium and assigned pygidium. Length of glabella, excluding occipital ring, 1.4 mm. Pygidial length 1.1 mm. UW A10924b,c, (p. 551)

13—Xenocheilos cf. *X. spineum* Wilson, 1951. Cranidium. Length 2.0 mm. UW A10924 (see fig. 4 and 6 above). (p. 560)

14—Iddingsia occidentalis DeLand & Shaw, n. sp. Holotype cranidium. Length 10.0 mm. UW A10920b. (p. 555)



1



2

3

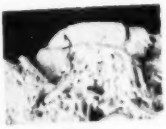
4

5

6

7

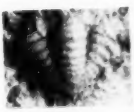
8



9

10

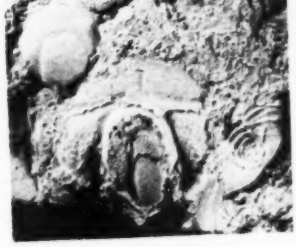
11

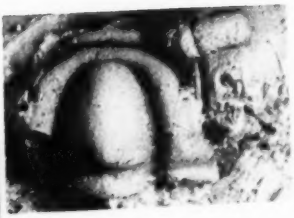


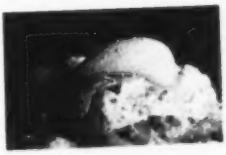
12

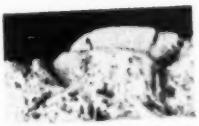
13

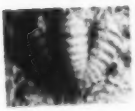
14

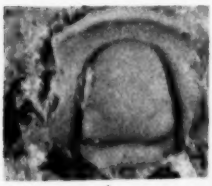






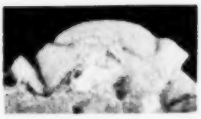






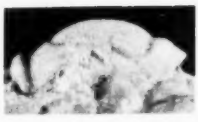
1

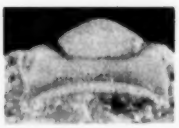
4



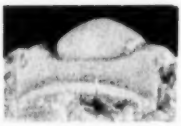
2

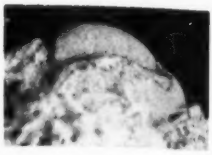
5





3





6

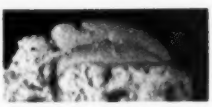
8

7

9

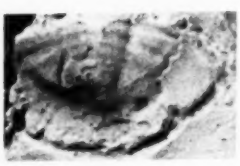
11

10

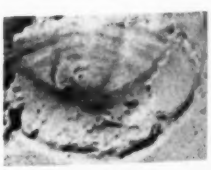


12

13



14



posterior width. Glabella highly convex, conical, anterior margin smoothly rounded, stands high above fixed cheeks, length slightly greater than or equal to width. In longitudinal profile, the glabella rises abruptly above occipital ring, then is smoothly convex with convexity increasing slightly toward the anterior end. Three pairs of faint glabellar furrows normal to the dorsal furrow distally and sharply curved back mesially; furrows not visible on all specimens even when coated or exfoliated. Occipital furrow broad and deep on inner surface of test, bowed forward slightly at center and at sides of glabella. Occipital ring short, convex, tapered and directed forward at the sides. Dorsal furrow broad, deep, complete. Preglabellar area from one-third to slightly more than two-fifths as long as glabella. Brim length ranges from slightly longer than border to twice as long as border with the smaller specimens possessing proportionately shorter brims than the larger. Brim moderately convex, nearly horizontal at dorsal furrow then steeply depressed to the deep, V-shaped marginal furrow. Radius of curvature of marginal furrow about two-thirds length of cranidium. Border arcuate, tapered, flat and slightly upsloping from marginal furrow. Fixed cheeks slightly convex, horizontal, about one-third width of glabella. Palpebral lobes gently curved, situated medially with respect to glabella. Palpebral furrow shallow. Ocular ridge faint, oblique, more prominent on small specimens. Posterior limb incomplete on all specimens collected, but at least two-thirds as wide as occipital ring, sharply depressed, marginal furrow broad and shallow on exfoliated specimens.

Facial suture cuts anterior margin about on a line with the palpebral lobes, curves sharply around antero-lateral corner of cranidium and trends straight back and inward to the anterior end of the palpebral lobe, which it rounds. Posterior course unknown.

Outer surface of test apparently smooth.

Free cheeks, thorax and pygidium unknown.

Remarks.—Variations in cranidial proportions exist within the population; the brim-border ratio varies from about 1.2 in the smallest specimen (glabella 2.4 mm. long) to 2.0 in the largest (the holotype, glabella 3.8 mm. long). The ratio of glabella length to width varies from 1.1 to 1.0 and is independent of glabellar length in the specimens measured.

This species differs from the genotype, *Dellea suada* (Walcott), 1890, in the higher convexity of glabella and brim and wider fixed cheeks. The glabellar convexity of *D. saginata* distinguishes it from other species of *Dellea* except *D. butlerensis* Frederickson, 1949, from which it varies in the greater convexity of the brim, higher brim-border ratio in mature specimens, wider fixed cheeks and longer radius of curvature of marginal furrow.

Locality and formation.—Seven cranidia from Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Holotype.—UW A10918a.

Paratypes.—UW A10918b–g, A10921.

EXPLANATION OF PLATE 66

All specimens are from the *Elvinia* zone of the Open Door limestone.

FIG. *1–3*—*Dellea* cf. *D. butlerensis* Frederickson, 1949. Three views of best cranidium. Length of cranidium 5.0 mm. UW A10912a. Loc. 32107/20B24. (p. 552)

4–7—*Dellea saginata* DeLand, n. sp. *4–6*, Three views of holotype cranidium. Length, excluding occipital ring 5.3 mm. UW A10918a. *7*, Exfoliated paratype cranidium. Length 5.1 mm. UW A10918c. Loc. 2997/27A10. (p. 552)

8,9—*Dellea suada* (Walcott), 1890? Dorsal and anterior views of cranidium. Length 5.6 mm. UW A10925. Loc. 32107/20B24. (p. 554)

10–12—*Irvingella* aff. *I. flohri* Resser, 1942. Three views of immature cranidium. Glabella, including occipital ring, 1.85 mm. UW A10922. Loc. 2997/27A10. (p. 556)

13—*Camaraspis plana* Frederickson, 1948. Three cranidia. ×0.865. UW A10909a. Loc. 32107/20B24. (p. 549)

14—*Housia vacuna* (Walcott), 1890?. Unique, fragmentary pygidium. ×2¼. UW A10923. Loc. 2997/27A10. (p. 555)

DELLEA SUADA (Walcott), 1890?
Pl. 66, fig. 8,9

Dellea suada (Walcott). WILSON, 1951, Jour. Paleont., vol. 25, p. 636–638, pl. 91, fig. 4–10,18, 20–23,25,26. (Complete synonymy to date)

A single cranidium seems to belong to *Dellea suada* or at least to be closely related to it as the species was revised by Wilson in 1951. One noticeable difference is the narrowness of the border in which the present specimen most closely approaches Wilson's fig. 6–8. A second difference is that *D. suada* has a finely granulated surface whereas the present specimen is punctate; the significance of this difference is not understood at present.

Distribution.—Steele Butte collection 32107/20B24 25–30 feet above the base of the Open Door limestone. *Elvinia* zone.

Plesiotype.—UW A10925.

Genus ELLIPSOCEPHALOIDES
Kobayashi, 1935
ELLIPSOCEPHALOIDES sp. indet.
Pl. 67, fig. 1

Description.—Cranidium transversely ovate, length about two-thirds width. Glabella cylindrical, convex, extending nearly the full length of the cranidium; anterior broadly rounded, two pairs glabellar furrows, anterior pair narrow, shallow and straight, posterior pair represented by deep pits on sides of the glabella. Occipital furrow straight, narrow and deep. Occipital ring long and flat at median axis, tapered laterally. Dorsal furrow rather narrow, well impressed. Brim very short, one-sixteenth length of glabella, nearly vertical. Width of fixed cheeks about one-third the glabellar width. Fixed cheeks slightly convex, nearly horizontal. Palpebral lobes broad, slightly curved, a little more than one-fourth of the glabellar length. Palpebral furrow broad and shallow. Ocular ridge well defined, marginal, merging with the brim at the anterior end, demarcated by a shallow furrow that connects posteriorly with the palpebral furrow. Posterior limb narrow, sharply depressed along the posterior margin.

Facial suture apparently intramarginal to the center since there is no trace of a border; directed sharply outward to and around the palpebral lobe, nearly normal to cranidial axis immediately posterior to palpebral lobe, then directed backward and outward to cut the posterior margin at a distance equal to one-fourth the width of the occipital ring from the dorsal furrow.

Outer surface of test covered with a network of fine subpolygonal ridges.

Free cheeks, thorax and pygidium unknown.

Remarks.—One nearly complete cranidium, 1.9 mm. long, undoubtedly representing an immature individual, is assigned to *Ellipsocephaloides*. It most closely resembles *E. montis* Resser, 1942, but differs in possessing a shorter brim, as would be expected in an immature cranidium, but specific identification based on a single juvenile specimen would be hazardous.

Locality and formation.—Sweetwater Canyon collection 2997/34A2, 131.6–131.7 feet above the base of the Open Door limestone. *Ptychaspis-Prosaukia* zone.

Figured specimen.—UW A10932.

Genus ELVINIA Walcott, 1924
ELVINIA sp. indet.
Pl. 67, fig. 9,10

Description.—Cranidium quadrate without posterior limbs, only slightly convex. Glabella conical, moderately convex, width slightly greater than length, anterior subtruncate, broadly rounded; one pair of moderately impressed, oblique glabellar furrows connected across the axis by a wide furrow. Occipital furrow wide and deep, bowed forward axially, shallower and directed forward laterally. Occipital ring moderately convex, directed forward laterally. Dorsal furrow complete, wide and deep. Brim about one-fifth as long as glabella, gently convex and downsloping; anterior part forms narrow, horizontal platform. Marginal furrow wide and deep, nearly straight. Border narrow, convex, nearly straight. Fixed cheeks nearly two-thirds as wide as the glabella, gently convex, downsloping; palpebral lobe unknown. Ocular ridge wide and strong, accentuated by the depression of the lateral extremities of brim. Posterior limbs unknown.

Outer surface slightly roughened.

Free cheek and thorax unknown.

Pygidium semicircular, length about one-half width, nearly flat except for high axis. Axis very slightly tapered, convex, extends

nearly full length of the pygidium; first three axial rings well defined by sharply incised furrows, fourth axial ring faintly demarcated from terminal segment. Dorsal furrow deep anteriorly, blends into marginal furrow at posterior end of axis. Pleural platform narrower than axial lobe, slightly convex; four segments, defined by deep interpleural grooves, extend to marginal furrow which is wide and deep. Border narrow, sharply upturned to a nearly vertical position.

Remarks.—This species was collected from the base of the Open Door limestone in all three of the sections discussed here. Collections consisted mostly of fragmentary cranidia or nearly complete pygidia; the most complete are illustrated. Unfortunately, none of the cranidia collected were complete enough to make specific identification possible.

Locality and formation.—Granite Falls collections 39113/5A5 (cranidium) and 39113/5A6 (cranidium and pygidium), 12.7 and 13.8 feet above the base of the Open Door limestone, respectively. Steele Butte collections 32107/20B24 (2 cranidia, 4 pygidia) and 32107/20B25 (pygidium), 25.0–30.0 and 33.0–33.6 feet above the base of the Open Door limestone, respectively. Sweetwater Canyon collection 2997/27A10 (cranidium, 2 pygidia), 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Plesiotypes.—UW A10907a, A10908a, A10913, A10915, A10916, A10927, A10928.

Genus HOUSIA Walcott, 1924
HOUSIA VACUNA (Walcott), 1890?
Pl. 66, fig. 14

Ptychoparia vacuna WALCOTT, 1890, U. S. Nat. Mus. Proc., vol. 13, p. 275, pl. 21, fig. 8–12.
Housia vacuna (Walcott). RESSER, 1936, Smithsonian Misc. Coll., vol. 95, no. 4, p. 23.
Housia vacuna (Walcott). WILSON, 1951, Jour. Paleont., vol. 25, p. 643–644, pl. 93, fig. 5–13.

Remarks.—The single pygidium tentatively assigned to this species has the anterior pleural segment with its diagnostic short spine still attached, although poorly preserved, and is marked by the characteristic fracture where the segment commonly separates from the pygidium.

Locality and formation.—Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Figured specimen.—UW A10923.

Genus IDAHOIA Walcott, 1924
IDAHOIA sp. indet.
Pl. 67, fig. 2

Description.—Pygidium semicircular, length about one-half width; axis no more than one-half the length of the pygidium; three axial rings and a flat posterior segment separated by wide, deep furrows. A downsloping ramp leads from the posterior segment to the concave border in a smooth curve. This ramp is not as wide as the posterior segment and is smoothly convex transversely. Pleural platform slightly convex, outer margin downsloping, three wide segments demarcated by broad, deep furrows. Posterior axial border concave, smooth, rest of border and marginal furrow unknown.

Locality and formation.—One pygidium and two cranidial fragments from Sweetwater Canyon collection 2997/27A12, 83.5–84.0 feet above the base of the Open Door limestone. *Ptychaspis-Prosaukia* zone.

Plesiotypes.—UW A10929, A11201.

Genus IDDINGSIA Walcott, 1924
IDDINGSIA OCCIDENTALIS DeLand & Shaw, n. sp.
Pl. 65, fig. 14

Description.—Glabella subcylindrical, evenly rounded in front, length slightly greater than width; in transverse profile, semicircular; in longitudinal profile, entire glabella is gently convex and raised above the occipital ring, convexity slightly greater along anterior one-third of glabella. Two pairs of glabellar furrows; anterior pair faint, oblique; posterior pair longer, well impressed, also oblique and curved posteriorly. Occipital furrow moderately wide and deep, deeper and curved forward laterally. Occipital ring slightly convex, tapered laterally, possessing a faint occipital node. Dorsal furrow wide and deep except immediately anterior to glabella where it is noticeably more shallow. Preglabellar area one-third length of cranidium divided subequally into a flat, horizontal border and a convex, downsloping brim by a wide shallow marginal furrow. A central swelling of the brim causes the marginal furrow to bow forward

centrally from its broadly curved course. Fixed cheeks about one-third width of glabella, faintly convex, sharply upsloping from dorsal furrow. Palpebral lobes one-half as long as glabella, broadly curved, posterior end opposite posterior end of glabella. Palpebral furrow well impressed. Ocular ridge prominent, oblique, reaches glabella well back of antero-lateral corner.

Facial suture apparently cuts anterior margin about on line with dorsal furrow, curves widely out and back to marginal furrow, then curves gently inward to the anterior end of the palpebral lobe, around which it curves. Further course not known.

Outer surface of test minutely granulose.

Remarks.—This species is much like *I. anatina* Resser, 1942, but differs in several minor, but consistent respects: (1) The sides of the glabella are parallel and not bowed as in *P. anatina*; (2) the occipital furrow is sharp and well incised rather than faint and shallow; (3) there is no occipital spine but only a barely perceptible node; (4) the border is shorter than in *I. anatina*; (5) the eyes are longer and less sharply curved; and (6) the convexity of the glabella is greater. In some respects this species resembles *I. simplicatus* Resser, 1942, too, but it differs in the glabellar convexity and shape, length of border and the lack of an occipital spine.

Locality and formation.—Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Holotype.—UW A10920b.

Paratypes.—UW A10920a,c, A10921.

Genus IRVINGELLA Ulrich & Resser, 1924
IRVINGELLA aff. I. FLOHRI Resser, 1942
Pl. 66, fig. 10–12

Description.—Cranidium semicircular, length about two-thirds width. Glabella stands high above fixed cheeks, very slightly tapered, width about three-fourths length, anterior broadly rounded. In longitudinal profile the posterior two-thirds of the glabella is flat and elevated above occipital ring; anterior one-third regularly convex. One moderately deep, oblique glabellar furrow is continuous across the glabella. Dorsal furrow complete, narrow and shallow. Occipital furrow narrow and deep; less deeply impressed and directed forward laterally. Occipital ring of normal length, convex, longest at center. Brim about one-tenth the length of the glabella, nearly flat and horizontal at dorsal furrow, rolled abruptly down at margin; anterior margin nearly straight. No border present. Fixed cheeks nearly as wide as glabella, convex and downsloping. Palpebral lobe widely curved about fixed cheek from opposite the occipital furrow to opposite anterior end of glabella, depressed below fixed cheek. No ocular ridge. Posterior limb short, narrow, bluntly triangular; marginal furrow broad and deep.

Facial suture intramarginal to center, indented slightly in front of palpebral lobe, broadly curved around palpebral lobes and directed sharply out and back to cut posterior margin within genal angle.

Outer surface of test finely granulated.

Remarks.—The single cranidium of this species is 2.1 mm. long and probably is an immature specimen. It most closely resembles *I. richmondensis* Resser, 1942, which seems to be based on young individuals of *I. adamsensis* and *I. flohri*; for these three "species" we choose the name *I. flohri* regarding the others as synonyms.

A comparison with specimens of *I. gibba* Miller, 1936, from North Fork Popo Agie River shows that *I. gibba* has a wider glabella and narrower fixed cheeks at a comparable cranidial size.

Locality and formation.—Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Figured specimen.—UW A10922.

Genus KINGSTONIA Walcott, 1924
KINGSTONIA SPICATA Lochman, 1940
Pl. 63, fig. 17

Kingstonia spicata LOCHMAN, 1940, Jour. Paleont. vol. 14, p. 34, pl. 4, fig. 1–9.

The pygidia in the present collection agree fully with the original description.

Locality and formation.—Steele Butte collection 32107/20B14 (2 pygidia) and 32107/20B15 (2 pygidia), 47.8–48.2 and 44.0–44.4 feet below the top of the Park shale, respectively. *Cedaria* zone.

Plesiotypes.—UW A10887, A10888a-d.

KINGSTONIA sp. indet.
Pl. 63, fig. 16

Description.—Pygidium semicircular, width slightly less than twice the length. Axial lobe two-thirds length of pygidium, narrow, slightly tapered, nearly flat, 6 narrow segments faintly demarcated by very shallow, wide, furrows. Dorsal furrow broad, shallow, faint around posterior margin of axial lobe. Pleural lobes slightly wider than axial lobe, gently convex, unsegmented except for broad anterior marginal furrow. Marginal furrow broad and shallow laterally, indistinguishable along the posterior axial margin. Border narrow, horizontal at furrow and rolled down abruptly to nearly vertical.

Outer surface smooth.

Remarks.—A single pygidium, complete except for the articulating ring, 3.8 mm. wide and 2.3 mm. long, is assigned to the genus *Kingstonia*. The lack of relief and the presence of what appears to be a marginal furrow may be due to crushing.

Locality and formation.—Steele Butte collection 32107/20B19, 20.4–20.6 feet below the top of the Park shale. *Cedaria* zone.

Figured specimen.—UW A10892.

Genus KORMAGNOSTUS Resser, 1938
KORMAGNOSTUS sp. indet.
Pl. 64, fig. 12,13

Remarks.—The fragmentary nature of the two pygidia and single cranidium collected preclude complete description. The following features, however, make the assignment of the specimens to *Kormagnostus* almost certain according to Lochman's (1940, p. 24) emended description:

(1) "... glabella convex, conical, consisting of a large posterior lobe and a small, low, sub-circular anterior lobe; ..."

(2) "... dorsal furrow wide, deep along sides of posterior lobe, joining the deep transverse furrow across front of lobe; dorsal furrow narrow, shallow, faint to obsolete around anterior lobe. ..."

(3) "Pygidium strongly convex; axial lobe wider than pleural lobes, expanding slightly on posterior half, extending to marginal furrow; anterior portion of axial lobe with a small central mode and marked by traces of two shallow furrows; ..."

Locality and formation.—Steele Butte collection 32107/20B15, 44.0–44.4 feet below the top of the Park shale. *Cedaria* zone.

Plesiotypes.—UW A10890a–c.

Genus LEIOCORYPHE Clark, 1924
LEIOCORYPHE sp. indet.
Pl. 64, fig. 1–3

Description.—Cranidium subhemispherical, highly convex, exfoliated but without a trace of any furrow, width greater than length but since posterior limbs are missing, the lateral extent of the cranidium in unknown. Posterior margin gently rounded, anterior margin semicircular. In longitudinal profile, the convexity of the cranidium increases posteriorly with the posterior margin of the cranidium vertical. In transverse profile the greatest convexity is along the median axis with the convexity decreasing toward the lateral margins. No trace of palpebral lobe.

Outer surface of test unknown; inner surface very finely punctate.

Locality and formation.—Steele Butte collection 32107/20B20, 10.5–10.6 feet below the top of the Park shale. *Cedaria* zone.

Figured specimen.—UW A10897.

Genus METEORASPIS Resser, 1935
METEORASPIS BOULDERENSIS DeLand, n. sp.
Pl. 63, fig. 18; Pl. 64, fig. 4–6

Description.—Cranidium subquadrate, length four-fifths width across posterior limbs. Glabella broadly conical, moderately convex, distinctly keeled, width at occipital ring slightly greater than length. Three pairs of shallow glabellar furrows, the posterior pair arcuate. Occipital furrow narrow and deep laterally, shallower on median line of glabella. Occipital ring narrow, convex, wider at axis than at extremities. Dorsal furrow narrow and deep, less deeply impressed in front of glabella. Preglabellar area about one-third glabellar length. Border twice as long at center as brim, moderately convex, arcuate. Brim sharply con-

vex, nearly vertical immediately behind deep marginal furrow. Two shallow pits within the marginal furrow in line with lateral dorsal furrows. Fixed cheeks about one-third width of glabella, moderately convex. Palpebral lobe of medium length, crescentiform. Palpebral furrow broad and deep. No trace of ocular ridge. Posterior limb almost as wide as occipital ring, triangular, depressed. Marginal furrow narrow and deep at junction with the dorsal furrow, becoming shallower laterally.

Facial suture appears to cut anterior margin about on line with dorsal furrow, moderately curved back to marginal furrow, then converges slightly to anterior corner of palpebral lobe, rounds palpebral lobe and curves gently out and back, curvature increases near lateral extremity to cut the posterior margin within the genal angle.

Outer surface finely granulated.

Free cheek, thorax and pygidium unknown.

Remarks.—This species differs from other described species of *Meteoraspis* in possessing a glabella which is wider than long and in the extremely narrow, nearly vertical brim; it is closely related to *M. keeganensis* Duncan, 1944, but differs in its stouter glabella.

Locality and formation.—Steele Butte collection 32107/20B19, 20.4–20.6 feet below the top of the Park shale. *Cedaria* zone.

Holotype.—UW A10891a.

Paratypes.—UW A10891b, A10895.

METEORASPIS ELONGATA Lochman, 1944
Pl. 64, fig. 9

Meteoraspis elongata LOCHMAN, 1944, in Lochman & Duncan, Geol. Soc. Am. Spec. Pap. 54, p. 98, pl. 9, fig. 4–7.

The original description is adequate, but the figured specimen displays the posterior limb for the first time.

Supplementary description.—Posterior limbs triangular, rather short, about three-fourths as wide as occipital ring, downsloping, nearly straight except for a faint upward flexure near the lateral extremity; posterior margin directed slightly backward laterally. Marginal furrow broad and deep.

Posterior to the palpebral lobe, the facial suture curves gently outward and backward, curvature increases toward the lateral extremity to give the posterior limb a sharply tapered appearance.

Remarks.—The single exfoliated cranidium belonging to this species has a suggestion of one pair of glabellar furrows represented by a flattening of the sides of the glabella opposite the posterior end of the palpebral lobe.

Locality and formation.—Steele Butte collection 32107/20B22, 2.7–4.2 feet below the top of the Park shale. *Cedaria* zone.

Figured specimen.—UW A10903.

METEORASPIS sp. indet.
Pl. 64, fig. 8

Description.—Glabella broadly conical, keeled, rounded anteriorly, no trace of glabellar furrows. Occipital furrow narrow and deep at sides. Occipital ring unknown. Dorsal furrow of medium width, deeper at sides than around anterior of glabella, complete. Brim about one-fourth length of glabella, slightly convex. Marginal furrow and border unknown. Fixed cheeks about one-fourth width of glabella, convex. Palpebral lobe medium length, slightly arcuate. Palpebral furrow medium width, well impressed. Ocular ridge broad, faint, obliquely directed toward a point well back of the anterior lateral corner of the glabella. Posterior limb triangular, depressed, about three-fourths as wide as glabella on same line, bears a broad, moderately well impressed marginal furrow. Surface of test covered with small irregularly spaced granules.

Remarks.—The proportions of the glabella and fixed cheeks resemble *M. elongata*, but because of the incompleteness of the single cranidium, specific identification is impossible.

Locality and formation.—Steele Butte collection 31207/20B20, 10.5–10.6 feet below the top of the Park shale. *Cedaria* zone

Figured specimen.—UW A10898.

Genus MODOCIA Walcott, 1924
MODOCIA CENTRALIS (Whitfield), 1877
Pl. 64, fig. 10

Modocia centralis (Whitfield). SHAW, 1956, Jour. Paleont., vol. 30, p. 141–144, fig. 1–4. Complete synonymy.

This species has been discussed by Shaw and a full synonymy given. Comparison of the present specimens with the data al-

ready presented shows that they belong in *M. centralis*.

Locality and formation.—Two cranidia from Steele Butte collection 32107/20B20, 10.5–10.6 feet below the top of the Park shale. *Cedaria* zone.

Plesiotypes.—UW A10896.

MODOCIA sp. indet.
Pl. 64, fig. 11

A single fragmentary cranidium is referred to the genus *Modocia*. It is probably *M. centralis*, but it is too fragmentary to permit measurement or comparison.

Locality and formation.—Steele Butte collection 32107/20B22, 2.7–4.2 feet below the top of the Park shale. *Cedaria* zone.

Figured specimen.—UW A10901.

Genus MONOCHEILUS Resser, 1937
MONOCHEILUS? sp. indet.
Pl. 67, fig. 2

Description.—Glabella slightly tapered, truncate anteriorly, bearing a median keel. Two pairs of shallow arcuate glabellar furrows of nearly equal length mark the middle third of the glabella. Dorsal furrows well impressed. Frontal limb convex, slightly downsloping, only slightly wider than the glabella; no distinguishable brim or border. Fixed cheeks apparently narrow. Palpebral lobes not preserved, but their roots suggest that they were rather long, somewhat over half the glabellar length. Surface apparently smooth. Other features unknown.

Remarks.—A single cranidial fragment could be assigned either to *Monocheilus* or to *Stigmacephalus*, for the distinctive palpebral lobes and posterior limbs are not preserved, but the poorly preserved inner edges of the free cheeks suggest long eyes like those of *Monocheilus*. The identification is extremely doubtful. Regardless of the generic assignment the specimen appears to represent a new species, for none of the species of either genus has such well developed glabellar furrows as this individual. No name is proposed, however, pending discovery of better preserved material.

Locality and formation.—Sweetwater Canyon collection 2997/27A12, 83.5–84.0 feet above the base of the Open Door limestone. *Ptychaspis-Prosaukia* zone.

Plesiotype.—UW A11201.

Genus TAENICEPHALUS Ulrich & Resser, 1924
TAENICEPHALUS CORDILLERENSIS Miller, 1936
Pl. 67, fig. 3,4

Taenicephalus cordillerensis MILLER, 1936, Jour. Paleont., vol. 10, p. 33–34, pl. 8, fig. 40, 41.
Taenicephalus cordillerensis Miller. RESSER 1942, Smithsonian Misc. Coll., vol. 103, no. 5, p. 101, pl. 19, fig. 33.
Taenicephalus holmesi RESSER, 1942, op. cit., p. 100, pl. 19, fig. 24–27.
Taenicephalus speciosus RESSER, 1942, loc. cit., pl. 20, fig. 19.
Taenicephalus wyomingensis RESSER, 1942, op. cit., p. 106–107, pl. 21, fig. 32.

Miller's original description of the cranidium is adequate.

Supplementary description.—Pygidium transverse, length about two-fifths width. Axis broad, slightly tapered, extends nearly full length of pygidium; four axial rings and a posterior segment separated by wide, deep furrows. Dorsal furrow wide and well defined. Pleural lobe triangular, convex, slightly downsloping at dorsal furrow, steeply deflexed at lateral extremities; the three segments do not extend onto narrow concave border. Interpleural grooves wide and deep. Marginal furrow absent, its position indicated only by a change in convexity.

Outer surface minutely granulated.

Remarks.—Resser has named several new species of *Taenicephalus* from Wyoming; these appear to be synonymous with *T. cordillerensis* in our present interpretation of the species. *T. holmesi* was characterized by bowed palpebral lobes and equal brim and border while *T. wyomingensis* had lower eyes and the brim longer than the border. These differences seem to be due to flattening of *T. wyomingensis*, which depressed the palpebral lobes and extended the frontal area. *T. speciosus* is based on a larger cranidium than the others and the distinctive features are those of *T. wyomingensis*. All of the characteristics mentioned by Resser can be regarded as due to preservation and not of taxonomic importance.

Locality and formation.—Four fragmentary cranidia and one incomplete pygidium are present in collection 2997/27A11, 53.4–54.0 feet above the base of the Open Door limestone at Sweetwater Canyon (UW

A10934). A single fragmentary cranidium which is tentatively assigned to this species occurs in collection 2997/34A1, 80.3–80.7 feet above the base of the Open Door limestone (UW A10933). *Conaspis* zone.

Plesiotypes.—UW A10933, A10934a–e.

Genus XENOCHEILOS Wilson, 1949

XENOCHEILOS cf. X. SPINEUM Wilson, 1951

Pl. 65, fig. 4,6,13

Xenocheilos spineum WILSON, 1951, Jour. Paleont., vol. 25, p. 649, pl. 95, fig. 15–17.

Description.—Cranidium quadrate, moderately convex. Glabella subcylindrical, width about 7/10 length, very slightly tapered anteriorly, broadly keeled, anterior smoothly rounded; no glabellar furrows. Occipital furrow of moderate width, deep, V-shaped, wider and directed forward at lateral extremities. Occipital ring convex, tapered laterally, stands above posterior portion of glabella, bears a low central node. Dorsal furrow wide, deep, and V-shaped except at postero-lateral corners and around anterior end of glabella where it is broad and shallow. Brim very gently convex and slightly downsloping, three times as long as the concave, arcuate border; marginal furrow indicated by change in convexity only. Fixed cheeks convex and upsloping which gives the glabella a sunken appearance. Width of fixed cheek and palpebral lobe unknown. Ocular ridge faint, at antero-lateral corner of glabella nearly normal to longitiudinal axis. Posterior limb depressed laterally and posteriorly, margins unknown. Marginal furrow deeper than any part of the dorsal furrow.

Facial suture appears to cut anterior margin well out from the center, curves sharply about antero-lateral corner of cranidium and is directed nearly straight back to anterior end of palpebral lobe. Further course unknown.

Outer surface of test smooth.

Free cheeks, thorax and pygidium unknown.

Remarks.—A single incomplete cranidium, 2.0 mm. long, closely resembles *Xenocheilos spineum* in proportions and convexity, but differs in the following respects:

(1) *X. spineum* has three pairs of glabellar furrows of which two pairs are usually visible. No furrows were observed on this cranidium.

(2) On *X. spineum* the anterior dorsal furrow is deeper than the posterior portion. On this specimen the anterior dorsal furrow is shallower.

(3) The ocular ridge is prominent on *X. spineum*, but it is faint on the figured head.

These differences might all be within the range of intraspecific variation. Only the collection of a number of specimens could establish whether a new species is warranted or not.

Locality and formation.—Sweetwater Canyon collection 2997/27A10, 1.0–1.5 feet above the base of the Open Door limestone. *Elvinia* zone.

Figured specimen.—UW A10924.

Genus and species undetermined

Cranidium A

Pl. 64, fig. 7

Description.—Glabella conical, abruptly tapered, length about equal to width at occipital furrow, gently convex anterior smoothly rounded; in longitudinal profile, posterior half flat, anterior gently convex; no glabellar furrows. Occipital furrow of medium width, shallow over axis of glabella, more deeply impressed at sides. Occipital ring broad, flat, bearing a median node. Dorsal furrow narrow and deep, less deeply impressed anteriorly. Brim nearly horizontal, very slightly convex. Relative length of brim unknown as are the features of the marginal furrow and border. Fixed cheeks flat, sharply upsloping from the dorsal furrow; width at anterior end of eye about three-fifths width of glabella, palpebral lobes about one-third the length of the glabella, gently curved, situated slightly posterior to glabellar median line and in the same horizontal plane as the crest of the glabella. Palpebral furrows faint. Broad ocular ridge directed obliquely from anterior end of palpebral lobe to antero-lateral corner of glabella. Extent of posterior limb unknown. Posterior margin directed slightly backward and gently downward. Marginal furrow deep and narrow.

Remarks.—This species, represented by a single fragmentary cranidium, appears to be

closely related to the genus *Bolaspidella* but differs from the genotype primarily in possessing narrower fixed cheeks. It may possess affinities to—"a *Deissella*-like genus"—mentioned by Howell & Duncan (1939, p. 3,4) as present in the lowermost Upper Cambrian of the Big Snowy Mountains, Montana. *Deissella* is considered congeneric with *Bolaspidella* by the present writers.

Locality and formation.—Steele Butte collection 32107/20B15, 44.0–44.4 feet below the top of the Park shale. *Cedaria* zone.

Figured specimen.—UW A10889.

Cranidium B
Pl. 67, fig. 7,8

Description.—Glabella quadrate, nearly as wide as long, very slightly tapered anteriorly, highly convex laterally, less so longitudinally, broadly rounded anteriorly. One pair of glabellar furrows, nearly straight, short, appear as triangular notches on the near vertical sides of the glabella. Occipital furrow broad and shallow axially, deeper and directed forward laterally. Occipital ring wide, convex, directed forward laterally but maintains equal length throughout. Dorsal furrow broad and deep at sides of glabella, less deeply impressed anteriorly. Brim, nearly horizontal immediately anterior to glabella, turning down abruptly to near vertical position. Marginal furrow and border unknown. Fixed cheeks unknown. Posterior limb about one-fifth wider than occipital ring, depressed posteriorly, bears a broad, straight, shallow marginal furrow.

Outer surface very finely granulated.

Free cheeks, thorax and pygidium unknown.

Remarks.—This species is represented by a single fragmentary cranidium. It resembles *Ptychaspis*, but the glabellar furrows of this specimen do not form transverse lobes as in *Ptychaspis*.

Locality and formation.—Sweetwater Canyon collection 2997/27A14, 184.0–185.0 feet above the base of the Open Door limestone. Trempealeauan, but faunal zone unknown.

Plesiotype.—UW A10931.

Cranidium C
Pl. 67, fig. 11–13

Description.—Cranidium subquadrate, nearly smooth, moderately convex, length about three-fourths width across palpebral lobes. In transverse profile cranidium is smoothly convex. In longitudinal profile the cranidium is regularly convex. Glabella very slightly raised above fixed cheeks, tapered, anterior margin undifferentiated; no glabellar furrows. Occipital furrow wide and shallow on inner surface of test. Occipital ring low, about as long as width of occipital furrow, apparently untapered. Dorsal furrow wide and shallow, not observable on anterior one-third of glabella. Preglabellar area not differentiated from glabella. Fixed cheeks about one-third the width of the glabella, continuing the glabellar convexity; palpebral lobes moderate in size, curved, situated slightly anterior to transverse median line of cranidium, palpebral furrow faint, no ocular ridge. Outer end of posterior limbs unknown, apparently strap-like; marginal furrow wide and shallow.

Outer surface of test smooth.

Free cheeks, thorax and pygidium unknown.

Locality and formation.—Four fragmentary cranidia from Sweetwater Canyon collection 2997/27A14, 184.0–185.0 feet above the base of the Open Door limestone. Trempealeauan, but faunal zone unknown.

Plesiotypes.—UW A10935a–d.

Pygidium A
Pl. 64, fig. 17,18

Description.—Pygidium transversely ovate, length three-fifths width, maximum width on a transverse line immediately posterior to axial lobe. Axis high, cylindrical, width three-fourths length, first two axial segments well defined by broad, deep furrows, third segment faintly demarcated from terminal segment. Dorsal furrow broad and shallow on outer surface of test but present only at sides. Pleural platform slightly convex, downsloping, three and possibly four segments separated by broad shallow pleural furrows, first furrow most deeply impressed. Border smooth, gently concave, nearly horizontal at margins, indented at posterior axial margin. Position of marginal furrow indicated on outer surface of test only by change in convexity.

Outer surface covered with minute granules.

Remarks.—A single, nearly complete specimen with the axial lobe exfoliated represents this species. Lacking associated cranidia, it cannot be referred with certainty to any genus although it resembles some species of such genera as *Uncaspis* or *Coosella* or some of the pygidia described from the Levis conglomerate by Rasetti.

Locality and formation.—Steele Butte collection 32107/20B14, 48.2–47.8 feet below the top of the Park shale. *Cedaria* zone.

Figured specimen.—UW A10886.

REFERENCES

DEISS, CHARLES, 1936, Revision of type Cambrian formations and sections of Montana and Yellowstone National Park: Geol. Soc. Am. Bull., vol. 47, p. 1257–1342, 2 pl., 10 fig.

——, 1938, Cambrian formations and sections in part of Cordilleran trough: Geol. Soc. Am. Bull., vol. 49, p. 1067–1168, 2 pl., 7 fig.

DELAND, C. R., 1954, Cambrian stratigraphy and faunas of the west flank of the Wind River Mountains, Wyoming (abstract): Geol. Soc. Am. Bull., vol. 65, p. 1373–1374.

HOWELL, B. F., & DUNCAN, DONALD, 1939, Middle-Upper Cambrian transition faunas of North America: Wagner Free Inst. Sci. Bull., vol. 14, no. 1, 10 p., 1 pl.

LOCHMAN, CHRISTINA, 1940, Fauna of the basal Bonneterre dolomite (Upper Cambrian) of southeastern Missouri: Jour. Paleont., vol. 14, p. 1–53, pl. 1–5.

——, 1950, Status of Dry Creek shale of central Montana: Am. Assoc. Petroleum Geologists Bull., vol. 34, p. 2200–2222.

MILLER, B. M., 1936, Cambrian Stratigraphy of northwestern Wyoming: Jour. Geol., vol. 44, p. 113–144, 10 fig., 5 tables.

RESSER, C. E., 1942, New Upper Cambrian trilobites: Smithsonian Misc. Coll., vol. 103, no. 5, 136 p., 21 pl.

SHAW, A. B., 1954a, Correlation of the Paleozoic formations of Wyoming: Wyoming Geol. Assoc. 9th Ann. Field Conf. Guidebook, Chart II.

——, 1954b, Cambrian of southern Wyoming (abstract): Geol. Soc. Am. Bull., vol. 65, p. 1386.

SHAW, A. B., & DELAND, C. R., 1955, Cambrian of southwestern Wyoming: Wyoming Geol. Assoc. 10th Ann. Field Conf. Guidebook, p. 38–42, 2 fig.

MANUSCRIPT RECEIVED JULY 13, 1955.

EXPLANATION OF PLATE 67

FIG. *1*—*Ellipsocephaloides* sp. indet. Unique cranidium. Width of glabella in front of occipital furrow 1.3 mm. UW A10932. Loc. 2997/34A2. (p. 554)

2—*Monocheilus?* sp. indet. and *Idahoia* sp. indet. Slab with fragmentary cranidia. ×1.1. UW A11201. Loc. 2997/27A12. (p. 557 & 555)

3,4—*Taenicephalus cordillerensis* Miller, 1936. *3*, Cranidium. Length of glabella, excluding occipital ring, 3.7 mm. UW A10934b. *4*, Assigned pygidium. Length (sag.) 4.1 mm. UW A10934c. Loc. 2997/27A11. (p. 559)

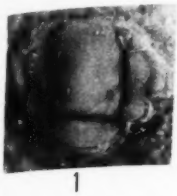
5—*Coosia dakotensis* Resser, 1942. Unique cranidium. ×1. UW A10905. Loc. 32017/20B23. (p. 551)

6—*Coosia connata* (Walcott), 1890? Fragment of cranidium. ×3½. UW A10906. Loc. 32107/20B23. (p. 551)

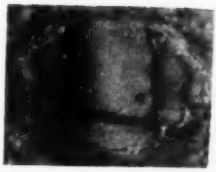
7,8—Cranidium B. Dorsal and antero-lateral oblique views of unique cranidial fragment. Sagittal length 4.2 mm. UW 10931. Loc. 2997/27A14. (p. 561)

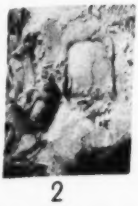
9,10—*Elvinia* sp. indet. *9*, Dorsal view of clay squeeze of cranidial fragment. ×1. UW A10915. Loc. 39113/5A5. *10*, Pygidium. ×1. UW A10907a. Loc. 32107/20B24. (p. 554)

11–13—Cranidium C. Three views of best cranidium. Length 5.0 mm. UW A10935d. Loc. 2997/27A14. (p. 561)


1

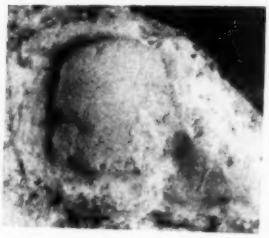
3

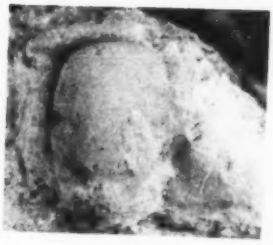


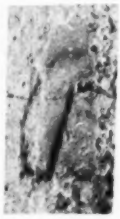

2

4

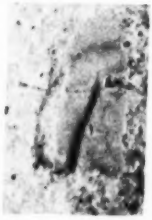
5


7



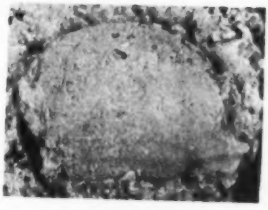

6

8



9

11

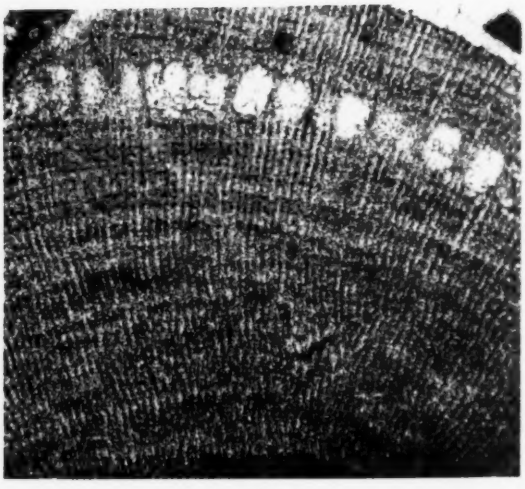


10

12

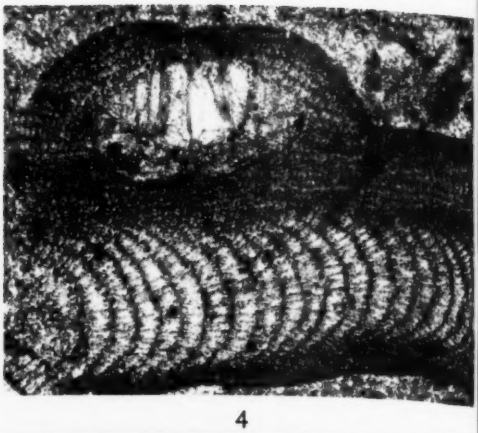
13

1

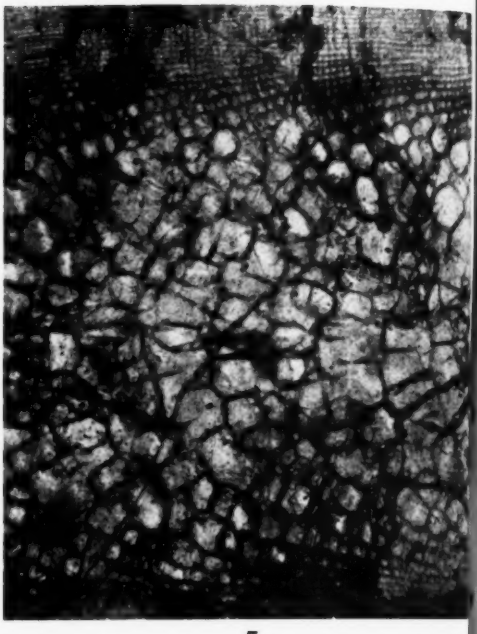


2

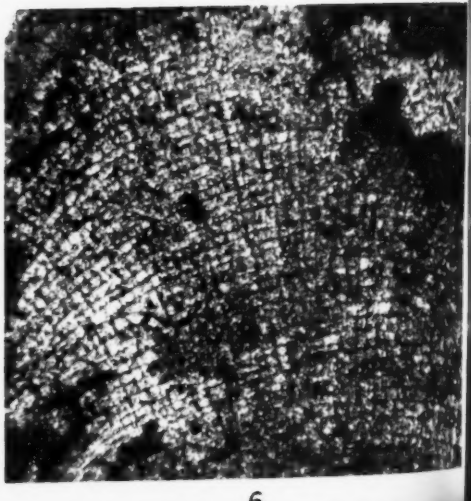
3



4



5



6

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 563–567, PL. 68, MAY 1956

ANCESTRY OF THE CORALLINE ALGAE

J. HARLAN JOHNSON
Colorado School of Mines, Golden, Colorado

ABSTRACT—Most of the Recent genera of coralline algae date back to the Late Cretaceous or Early Tertiary. Little is known regarding their ancestry. The view has been generally held that the ancestral stock was to be found in the Paleozoic family Solenoporaceae. The primitive genus *Archaeolithothamnium* was supposed to represent a transitional stage between the solenoporaceas and the more highly developed Recent genera.

It is, therefore, highly interesting to note that some Pennsylvanian algae recently studied show structures much more closely allied to the Recent genus *Lithophyllum* than any known among the Solenoporaceae. These structures include well-defined hypothallic and perithallic tissues, a co-axial hypothallus, and conceptacles of sporangia.

Other recent finds from Lower Pennsylvanian limestones include abundant debris of a form having structural features suggestive of articulated coralline algae.

It is suggested that the separation of the two types of coralline algae (the crustose and the articulated) may date back to Paleozoic times, and that the two main groups of the crustose corallines (*Lithothamnium*-type and *Lithophyllum*-type) are equally ancient.

THE view has been held generally that the ancestral stock of the modern coralline algae was to be found in the Paleozoic family *Solenoporaceae*. Madame Lemoine (1911, p. 184–187) pointed out that among the species of *Solenopora* described from the Paleozoic, two groups could be easily distinguished on the basis of structure. One, in which the layers of cells were the basic element, another in which the vertical rows were the predominating structure. She also noted that a study of the illustrations of earlier articles proved that, at least some of the species had a poorly developed basal hypothallus consisting of a few curved rows of cells similar to that typical of the genus *Lithothamnium*. Studies of the genus *Archaeolithothamnium* led her to believe that very probably it represented a transitional form between the Solenoporaceae and the modern genera of crustose coralline algae. In 1917, the same author (p. 237–239) reviewed the subject and presented additional data. She emphasized that while, superficially, the external appearance and general structure of Paleozoic *Solenopora* closely resembled those of the crustose coralline algae, the majority of the *Solenopora* differed greatly from any of the modern genera of the crustose algae by the size of the cells. In general, the cells of the Paleozoic *Solenopora* are vastly larger than those

EXPLANATION OF PLATE 68

FIG. 1—*Lithothamnium limaensum* Johnson and Tafur. Eocene, Peru. Shows hypothallus, perithallus and a cavity representing a conceptacle chamber. Note the vertical cell rows and growth zones. ×100.

2—*Archaeolithothamnium* sp. Pleistocene, Okinawa. Shows a section of perithallic tissue and numerous sporangia. Note the vertical cell rows and suggestions of growth zones. ×100.

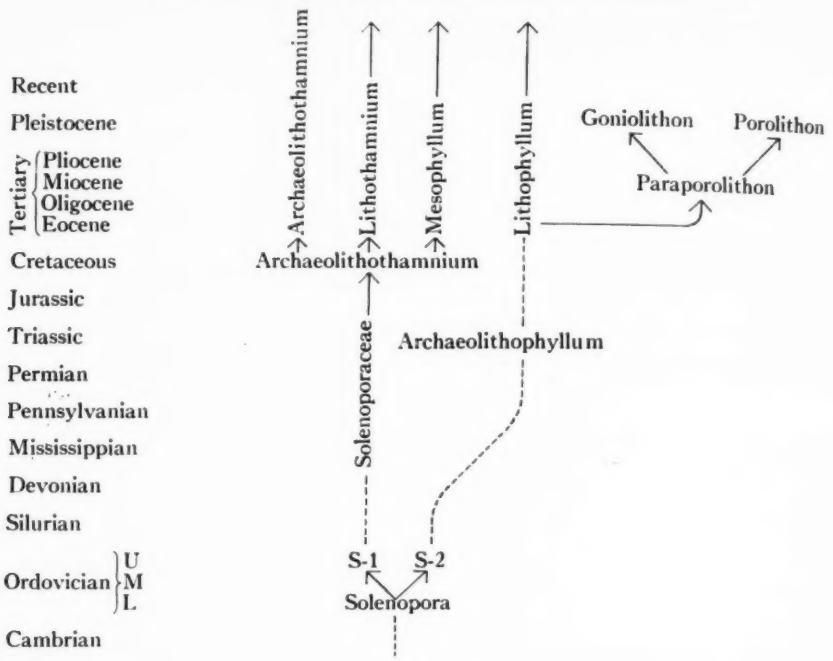
3—*Solenopora* sp. Mississippian (St. Genevieve), Missouri. A section of the perithallic tissue showing the vertical cell rows and growth zones. ×50.

4—*Ltihophyllum* sp. Miocene, Saipan, M.I. A section showing hypothallus, perithallus, and a conceptacle containing sporangia. ×125.

5—*Archaeolithophyllum missourieum* Johnson. Pennsylvanian, Illinois. Note the well defined hypothallus and perithallus, and the large polygonal hypothallic cells. ×50.

6—*Solenopora* sp. Devonian, Alberta. Shows a very regular tissue with well defined cell layers. ×40.

SUGGESTED FAMILY TREE OF THE CRUSTOSE CORALLINE ALGAE



found in any of the modern crustose coralline algae. In this respect, they more closely resembled the cells of some of the articulate coralline algae.

Other features which have made difficult a consideration of the *Solenoporaceae* as ancestral corallines have been the slight differentiation of their tissue into hypothallus and perithallus, and the lack of recognizable reproductive organs.

Several authors have mentioned a differentiation of tissue, but their illustrations show such developments to have been very slight at best. This is true, not only for Paleozoic material, but for Mesozoic species as well. Some specimens and certain species do show slight suggestion of differentiation of hypothallus and perithallus, particularly among the branching forms of the Late Mesozoic. However, this differentiation is not nearly so well defined as in any of the modern genera of coralline algae.

The same is true of reproductive organs. The vast majority of the *Solenopora* studied to date show no indications whatever of such structures. Pia (1930, p. 130) assumed that probably they were external, not calcified, and consequently were not preserved. A very few forms have been found which showed some irregularities in the tissue that have been interpreted by various authors as reproductive organs. This evidence has recently been summarized by Wood (1944) with additions by Garwood (1945). The total evidence, if taken at face value, would suggest that rarely they may show some small spindle-shaped sporangia, but no well-preserved specimens definitely showing such features have yet been found among the *Solenopora*.

Lemoine in her 1917 paper concludes that a few species of *Solenopora* do show structures which appear to be intermediate between the typical *Solenopora* and the genus *Archaeolithothamnium*, and elsewhere in the paper she concludes that in all probability *Lithothamnium*, *Lithophyllum*, and other genera descended from different types of Cretaceous *Archaeolithothamnium*. Certainly, Pfender (1926) described a number of Cretaceous species of *Archaeolithothamnium* which included a variety of structural features.

Pia (1937, p. 799) reviewed the question

and expressed the same opinion, namely, that both *Lithothamnium* and *Lithophyllum* were derived from certain species of *Archaeolithothamnium* which in turn developed from some of the Solenoporaceae. Therefore, it is of great interest to note that some Pennsylvanian algae recently studied (Johnson, 1956) show forms having well-developed and distinct hypothallic and perithallic tissue. It was somewhat of a surprise to the writer to note that hypothallic structure of one of these groups is coaxial, that is, formed of arched layers of cells. This is a structural feature which characterizes the genus *Lithophyllum* and which is well developed among all the modern articulate coralline algae. One would have expected to find a hypothallus consisting of the simpler, curved cell layers similar to that of the modern *Lithothamnium* which presumably is the more primitive structure. This material has been described by the author as a new genus to which he has given the name *Archaeolithophyllum*. It has been found widely distributed at certain stratigraphic horizons of the Pennsylvanian in Texas, Kansas, Missouri, and Illinois. Several species have been recognized.

Also of interest is the fact that there is in *Archeaolithophyllum* distinct evidence of the presence of conceptacles, a structural feature not found in any previously described Paleozoic algae. Of additional interest, is the fact that these conceptacles, instead of being large and wide as in *Lithothamnium*, are relatively small and highly arched, strongly suggesting the presence of a single large aperture rather than numerous small ones. This again is not the primitive type of structure to be expected in such an ancient genus. As stated earlier, the hypothallic tissue of *Archaeolithophyllum* shows coaxial structure, that is, the arched layers of cells. However, the individual cells of the hypothallus are polygonal and are much larger than those found in the present-day corallines; in other words, they strongly suggest, both in size and the polygonal outline, cells of some of the *Solenopora*. The perithallic tissue, on the other hand, is formed of layers of small rectangular cells of about the same size as those found in Recent species of *Lithophyllum*.

As nearly as can be determined from the fragments, *Archaeolithophyllum* was a crustose plant forming irregular plates or sheets from which, in some specimens at least, small protuberances or even short branches developed. In a few cases, the plants appeared to have encrusted other organisms or fossil fragments.

Little is known regarding the ancestry of the articulated coralline algae. The common genera *Corallina*, *Amphiroa*, and *Jania* appeared in the Late Cretaceous or early Eocene. No fossils showing structures suggestive of ancestral forms have yet been described from earlier rocks.

Another recent find of algal remains in Lower Pennsylvanian rocks of west Texas and adjoining areas in New Mexico have brought to light a form having structural features strongly suggestive of some of those found among the articulated coralline algae. Unfortunately, the material is very fragmental, but it suggests a plant having long, slender branches which are circular or oval in cross section. The fragments are composed largely of strongly arched rows of rectangular to polygonal cells. Frequently, these are somewhat wedge-shaped in section, and a casual glance at the tissue strongly suggests those to be observed among the modern *Jania* and *Amphiroa*. This Pennsylvanian material has not yet been described.

On the basis of information now available, it is suggested that the two main divisions of the coralline algae, that is, the articulated and the crustose types, date back into Paleozoic times, possibly even as far back as the Late Mississippian. It is suggested that the articulated coralline forms begin as small bushy branching plants which originally were not calcified, but with the development of the calcified habit, articulation began as a structural feature to permit the plants to remain highly flexible. Little more can be said about them until considerably more fossil material is obtained, without entering into the realm of hypothesis.

In her classic work of 1911, Madame Lemoine pointed out that all modern coralline algae can be divided into two groups according to the basic arrangement of cells in the tissue of the plant. In Group I (the *Lithothamnium*-type) the basic structure consists of vertical rows of cells. The cells in adjoining rows are not at the same

level. In Group II (the *Lithophyllum*-type) the basic structure is a horizontal layer of cells which in vertical section appears as a horizontal or slightly curved row of cells. The cells in adjoining layers may or may not be in corresponding positions so that the end partitions form a continuous line. We have already mentioned that among the early *Solenoporaceae*, of the Later Ordovician and Silurian, we find among the number of species that have been described some which show structures corresponding to the first group and some which have cell arrangements corresponding to those of the second.

Among Recent algae, those belonging to Group I normally have a rather simple hypothallus consisting of curved rows of cells, while those belonging to the second commonly have a coaxial hypothallus. As far as is known at the present time, all of the Solenoporaceae, both Paleozoic and Mesozoic, have a simple basal hypothallus of the first type. None of them shows a coaxial hypothallus. The same is true in the genus *Archaeolithothamnium*. The majority of the Mesozoic *Solenopora* have the basic cell arrangement of Group I, although some of the later ones have developed a very regular perithallus.

The genus *Archaeolithothamnium* appears rather early in the Cretaceous and by the end of the Cretaceous is represented by a large number of species which show a considerable diversity of structure. All of them have a simple hypothallus characteristic of Group I. A number of them also have the basic cell arrangement in vertical rows. However, in some, the cells in the individual rows become so uniform in size that the tissue has an extremely regular appearance, suggestive both of vertical rows and horizontal layers. Some of the Late Cretaceous species develop a highly branching form of which the branches show a differentiation into a medullary hypothallus and a marginal perithallus which is very similar to that seen among some of the branching *Lithophyllum* and in *Mesophyllum*. However, identical structures can be found among some of the recent branching *Lithothamnium*.

The reproductive organs of the *Solenopora* are not known. Presumably, as suggested by Pia (1930, p. 130) they were external sporangia. In *Archeaolithothamnium* these sporangia are internal, developing just under the external surface of the plant. They consist of individual sporangia which are usually separated by one or more layers of perithallic tissue. Among the *Lithothaminum* the sporangia are quite similar in appearance but, instead of occurring separately in the perithallus, they have been collected into large conceptacles of sporangia which have many apertures. In some cases, at least, there appears to be an aperture for each individual sporangium.

It is thus quite easy to visualize the gradual evolution of plant structure from a *Solenopore* of the first type through *Archaeolithothamnium* and on into *Lithothamnium*. There would be little or no change in the basal hypothallus. There would be a decrease in the size of the cell from the *Solenopora* into the *Archaeolithothamnium*, particularly in the perithallic tissue. The sporangia which at first were external gradually became immersed in the tissue with only the external pore projecting at or above the surface. Then the sporangia collected in groups ultimately being enveloped by a conceptacle. The earlier conceptacles were probably very large, nearly flat roofed, and pierced by many apical pores. Later, the tendency was to develop smaller, more highly arched conceptacles with a reduced number of apical pores.

Along the way undoubtedly there were a number of side lines developed, some of which may have been temporarily important locally.

With Group II, starting back in the Ordovician with species of *Solenopora* such as *S. fusiformis*, *S. compacta*, or *S. lithothamnionides*, in which structurally the cells were arranged in concentric layers, we can visualize another series of evolutionary trends. The curved layers of cells which formed the basal hypothallus eventually developed into a coaxial hypothallus. Above, this, the cell layers become more and more uniform in the arrangement of the cells until ultimately the cells in section would appear to be regularly arranged in a lattice pattern. This would result in a clear-cut distinction between the basal hypothallic tissue and the perithallus. With that would come a re-

duction in the cell size at first among the cells of the perithallus, later in the hypothallus, with a tighter packing of the cells in the perithallic tissue. The tendency would be to change from a polygonal or rounded cell to a rectangular cell.

The sporangia, originally external, gradually were collected into relatively small clusters developing into internal sporangia which with time became smaller and in some cases more and more immersed within the tissue. Originally each sporangium had a pore at the end. As the sporangia collected in clusters and later into small rounded conceptacles, the number of apertures or canals for the escape of spores became less and less until finally one large opening sufficed for all. We can thus visualize an evolution from some of the Solenoporaceae of Group II through *Archaeolithophyllum* into *Lithophyllum*.

REFERENCES

GARWOOD, E. J., 1945, Note on the organs of reproduction in *Solenopora gracilis:* Geologists' Assoc. (London) Proc., vol. 56, pt. 3, p. 147–148, pl. 5.

JOHNSON, J. H., 1956, *Archaeolithophyllum.* A new genus of Paleozoic coralline algae: Jour. Paleont., vol. 30, no. 1, p. 53–55, pl. 14.

LEMOINE, MME. PAUL, 1917. Contribution à l'étude des Corallinaces fossiles. 1. Généralitiés sur la structure des corallinacées: Soc. géol. France Bull., 4th ser., vol. 17, p. 233–240.

——, 1911, Structure anatomique des Mélobésiées. Application a la classification: Inst. Oceanographic Monaco, Ann., vol. 2, no. 1, 215 p., 105 fig., 5 pl.

PFENDER, J., 1926, Les Mélobésiées dans les calcaires Crétacés de la Basse-Provence: Soc. géol. France, Mém. n. ser., vol. 3, fasc. 2, Mém. no. 6, 31, p., 10 pl.

PIA, J. VON, 1930, Neue Arbeiten über fossile Solenoporaceae und Corallinaceae: Neues Jahrbuch, vol. 3, p. 122–147.

——, 1937, Die wichtigsten Kalkalgen des Jungpaläozoikums und ihre geologische Bedeutung: 2e. Cong. études Stratig. Carbonif. 1935, Comptes rendus, vol. 2, p. 765–856, 2 figs., 13 pl.

WOOD, A., 1944, Organs of reproduction in the Solenoporaceae: Geologists' Assoc. (London) Proc., vol. 55, pt. 2, p. 107–113, 2 fig., pl. 5–6.

MANUSCRIPT RECEIVED JANUARY 19, 1956

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 568–607, PL. 69–72, 27 TEXT-FIG., MAY 1956

TERTIARY ANACANTHIN FISHES FROM CALIFORNIA AND THE PACIFIC NORTHWEST; THEIR PALEOECOLOGICAL SIGNIFICANCE

LORE ROSE DAVID
The John Crerar Library, Chicago

ABSTRACT—All Anacanthini found from Eocene through Pliocene sections of California, Oregon and Washington are described. This order of almost entirely deep-water fishes is represented by 32 species belonging to 16 genera and five families. Anacanthini are most abundant and varied in deep-water deposits of the Refugian, and from the Zemorrian to lower Saucesian stages. They are absent in the Relizian and Luisian, and reappear in some Mohnian, Delmontian and Pliocene strata. Paleoecologic conditions of deposition of each described species and faunal assemblages accompanying it are considered at length. These approximate conditions indicated by Foraminifera occurring in the same formations. Conditions of deposition of Recent fish remains are discussed considering the particular circumstances under which assemblages may accumulate.

The following 26 new species are described (the 13 new genera which are described are indicated by their type species marked*): *Paleobathygadus oligocenicus**, *P. yaquinensis*, *P. careagrus*, *P. zemorrianus*, *P. wilmingtonensis*, *Probathygadus keaseyensis**, *Progadus pliocenicus**, *P. miocenicus*, *Promacrurus zemorrianus**, *P. oregonensis*, *P. newmanni*, *P. alseanus*, *P. alferitziensis*, *P. asymmetricus*, *P. saucesianus*, *P. mimus*, *Pyknolepidus macrospinosus**, *Homeonezumia multispinosus**, *Amblygoniolepidus polystichus**, *Oxygoniolepidus washingtonensis**, *Homeocoryphaenoides chiasmacanthus**, *Calilepidus tauxei**, *Leptacantholepidus delmontianus**, *L. rotundus*, *Homeomacrurus fernandensis**, *Promerluccius venturaensis**.

INTRODUCTION

THE abundance of anacanthin fishes, particularly of members of the family Macruridae, in certain deposits of California, Oregon, and Washington, is striking. In numerous Tertiary fish scale assemblages from these states the dominant forms are macrurids, a group known among Recent fishes as the "herrings of the deep sea" because their abundance in the depth of the ocean equals the distribution of herrings in shallower pelagic waters. These occurrences viewed in relation to the known Tertiary fish fauna of this region, comprising many neritic and shallow-water forms, is of special interest. Mixed occurrences of macrurids with coastal neritic forms are not unique to the Pacific coast of America. Similar assemblages have been described from many other regions (from the Mediterranean Sahélian, Arambourg, 1925, 1927; Erasmo, 1927–1929, 1930; from the Toscana Pliocene, Pieragnoli, 1919; from the Wiener Becken, Schubert, 1905–1096, 1912; from Teritary deposits of Rumania, Northwest Germany, and Holland, Weiler, 1942, 1949). Weiler (1949) has pointed out the paleoecological significance of these fish assemblages. In attempting to give a satisfactory explanation for the association in fossil assemblages of fish forms of such different habitats, he concludes that macrurids must have been inhabitants of shallower water during the late Tertiary. In view of observations on Tertiary fish scale assemblages in California and the Pacific Northwest this conclusion seems unlikely. An analysis of anacanthin occurrences on the Pacific coast is presented here. All material of this order available from the Pacific coast is described and the paleoecology of each of the localities where Anacanthini occur is studied, considering other forms found at the same spot. In general Pacific coast assemblages in this report are classed into four ecological types: In *shallow neritic* facies no macrurids and usually no anacanthin fishes at all are found: in *deep neritic* facies anacanthin fishes are rare or absent; in assemblages considered as *bathyal*, or *abyssal*, anacanthin fishes (particularly macrurids— are usually abundant or dominant, while a restricted number of neritic forms may occur, represented in small number each, and often fragmented. Herrings and round-herrings are the most

abundant forms and either one or both occur to some degree in all assemblages.

Even though fairly large collections of these fish scale assemblages exist in the vertebrate paleontology department of the California Institute of Technology, in various oil company laboratories and in the author's possession, very little of the material has been described. Illustrations of index fossils (David, 1944, 1946, 1947b and 1948) may be helpful in verification of most of the forms given in the faunal lists below.

FOSSIL MATERIALS USED

The fish scale assemblages were taken from a definite depth of well cores as shown for each type, or came from corresponding outcrops representing complete series of depositions over a great length of time. Such exact information as is available for material collected in oil well cores, offering definite information as to depth of strata and most often correlation with foraminiferal zones of neighbouring wells and outcrops, provides a great advantage for paleoecological determinations.

All anacanthin forms are readily definable as to family and species. Scales of the families Bathygadidae, Gadidae, Merlucciidae, Bregmacerotidae, and Macruridae are distinctly different from each other and can not possibly be mistaken for scales of any other groups of fishes, if we disregard very few exceptions with degenerate scales. The family Macruridae, especially, offers a great many distinctive scale traits which can be used for species determinations (Gilbert & Hubbs, 1916, 1920; Peabody, 1931; Parr, 1946). All fossil forms could be included in living families of anacanthin fishes. Combining of various species into generic units corresponding to the genera of living forms does not seem possible. Even though some of the fossil forms approach the characteristics of the scales of living genera fairly closely, the descriptions show that sufficient differences exist in all cases to warrant the designation of all fossils here described to new genera and species. Wherever possible, new genera were compared with related living forms. In some cases fossil genera and species are too far removed from all known living forms to attempt comparison with specific living forms.

All types of new species are preserved in the collection of vertebrate paleontology of the California Institute of Technology, if not otherwise stated. Type nembers are given as "CIT ———" standing for that institution and the number of the type. Measurements are given as "–·– by –·– mm" meaning –·– by –·– mm length to depth of the scale. In some cases the length of the protruding apical spines is added to the length of the scale as: –·–+–·– by –·– mm.

A diagram of a fish scale and descriptive terms are found in David, (1944), p. 28. Basal and anterior margin, and apical and posterior margin, respectively, define identical structures. The distance between basal (anterior) and apical (posterior) margins is termed "length of scale"; that between dorsal and ventral margins is the "depth of the scale." All scales shown are representative of the dorsal portion of the flanks of the fish, ventral to the dorsal fins.

ACKNOWLEDGMENTS

The fossil materials from the Pacific Northwest described in this report were collected during a field trip sponsored by the U. S. Geological Survey and were furnished to the author by Dr. A. Mayers, Princeton University, upon suggestion of Dr. Harry Ladd, U. S. Geological Survey, Washington, D.C. It is a pleasure to thank Dr. Myers and Dr. Ladd for the efforts made in supplying this material. Most of the California material was collected during investigations conducted in 1941–42 using the facilities of the paleontological laboratory of the California Institute of Technology, Pasadena. Acknowledgement is made to Tom Rothwell, paleontologist of the Richfield Oil Corporation for supplying some additional material contained in the collections of that corporation. Sincere thanks are due also to the Oceanographic Institute and the Marine Biological Laboratories, Woods Hole, Massachusetts, for offering laboratory and library facilities during the summer of 1950. I thank the Oak Ridge Institute of Nuclear Studies, Oak Ridge, Tennessee, for the use of their library and laboratory space during the years 1951 to 1954.

SYSTEMATIC PALEONTOLOGY

Family BREGMACEROTIDAE

Pl. 69, fig. 1

BREGMACEROS KREYENHAGUS David

Text-fig. 1

Bregmaceros kreyenhagus DAVID, 1946, Carnegie Inst. Washington, Pub. 551, no. 4, pl. 1, fig. 5.

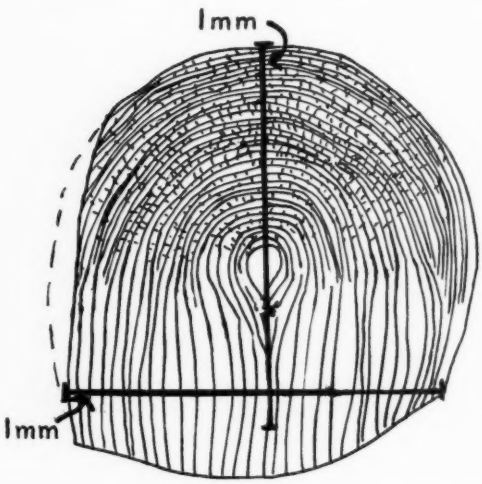
Bregmaceros seems to be represented by one species only, which was described earlier (David 1946, p. 62–63). This species is characteristic for the upper Eocene of California and probably the same species occurs in Oregon. Pl. 69, fig. 1 shows a scale of *Bregmaceos atlanticus* Goode & Bean from Tortugas, Fla.; Text-fig. 1 shows a scale of *B. kreyenhagus* from the Western Gulf, Lillis Welch No. 1 well, at 2009–2100 ft. depth.

Family BATHYGADIDAE

Pl. 69, fig. 2–4

Scales of two living species were studied: *Bathygadus antrodes* Jordan & Gilbert from *Albatross* Expedition Station 5083, and *Gadomus* (?*Bathygadus*) *longifilis* (Goode & Bean) *Albatross* Expedition Station 2392, at 734 fathoms depth. These agree well with the scales of the two species described by Peabody (1931), *B. sulcatus* (Smith & Radcliffe) and *B. filamentosus* (Smith & Radcliffe).

Bathygadid scales show the following characteristics: The apical circuli, concentric with the apical margin, are either uniformly rounded or have one or several angulated folds. The nucleus, central or slightly basad, is rounded to pear shaped. The dorsal and ventralmost circuli may run vertically from basal to apical margin not continuing around the entire apical border. The scales widen towards the basal border; the intercircular spaces widen conspicuously towards the basal region. The central basal circuli form sharp pointed angles in the median axis of the basal pole; occasionally the basal circuli meet slightly asymmetrically at one side of the midaxis. Dorsal and ventral to the axis the basal circuli end diagonally towards the basal border directed towards the center. The angulation and the concentricity of the basal circuli may become very irregular towards the basal margin; several angles may be formed by some circuli and these are not always concentric with the neighboring ones. A checkerboard appearance of the apical portion of the scales is caused by short radial lines crossing the apical circuli and dividing the intercircular spaces into numerous small spaces. Wavy edges or pustulate markings characterize the edges of the basal circuli. The scales vary in size. *B. antrodes* is larger, the scales measured 2.8 by 2 and 2.29 by 2.67 mm., a lateral line scale measured 5 by 4.67 mm.; *G. longifilis* was represented by scales of 2 by 2 and 4 by 3.5 mm.



TEXT-FIG. *1—Bregmaceros kreyenhagus* David from the Western Gulf Co. well Lillis Welch No. 1, at 2009 to 2100 ft. depth; 1.1 by 1.07 mm.

The only forms to which the Bathygadidae show a superficial similarity in their scales are the deep-water Gadidae. The distinguishing characteristics of the Bathygadidae as compared to these are the sharp median angles of the basal circuli as compared to the more or less parallel central basal circuli of the Gadidae, where only rarely one or a few of the most central circuli may meet in deeply extended angles and dorsal and ventral basal portions are generally divided by a smooth median groove. The checkerboard-like pattern of the apical region was never found in gadid fishes (Pl. 69, fig. 5–8; pl. 70, fig. 1–3).

Genus PALEOBATHYGADUS, n. gen.

Type species.—Paleobathygadus oligocenicus n. sp.

The fossil genus is distinguished from the

scales of the living forms by the rounded shape of the scales; the wide, rounded apical pole; and the central adapical nucleus.

PALEOBATHYGADUS OLIGOCENICUS, n. sp.
Text-fig. 2

Holotype.—CIT 10421; 2 by 2.5 mm.

Type locality.—Fred Jasper Oil Co., Fred Jasper No. 1 well, Sec. 16, T. 26, S., R. 27 E., Mt. Diablo B. & M., San Joaquin Valley, California, at 4075–4104 ft. depth.

Paratypes.—CIT 10422–10435, 14 specimens; 1 by 0.67 mm. to 2.33 by 2.67 mm. from the same locality, at depth from 4075–4101 ft.

Description.—Scales mostly deeper than long, almost rounded with concentric rounded circuli in apical region; some specimens with slightly angulated circuli in area of apical pole, but apical pole always wide. Nucleus pear shaped, central or approaching basal region. At least 7 to 10 circuli forming acute angles towards median axis of basal region. Intercircular spaces widening comparatively little towards basal region; 15 to 16 in 1 mm. dorsoventrad across basal region as compared to 18 circuli in 1 mm. apicobasad through apical region. Basal circuli comparatively regular, mostly parallel to each other, external circuli ending diagonally towards basal border, becoming more and more vertical in basoapical direction towards outer border of scale. Checkerboard pattern very distinctly marked in apical region, remarkably so, considering that these rather fine markings are so distinguishable in the fossil state. Scales very coarse.

The species is distinguished from all others of the genus by its coarseness, the distinctness of the checkerboard pattern, the evenness of the intercircular spaces and the rounded appearance of the apical pole.

In the Fred Jasper well, *P. oligocenicus* occurs with the Saucesian-Zemorrian *Etringus*. The remaining fish scales have not been determined and are at the time not available.

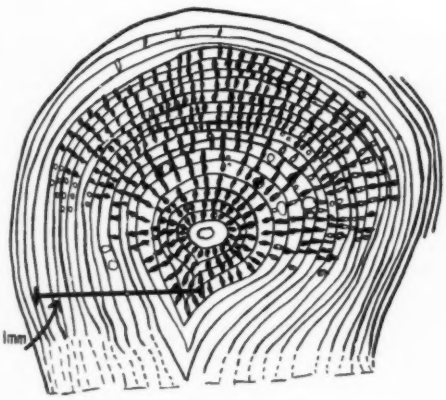
PALEOBATHYGADUS YAGUINENSIS, n. sp.
Pl. 71, fig. 1–2; Text-fig. 3

Holotype.—CIT 10436, 2.3 by 2.67 mm.

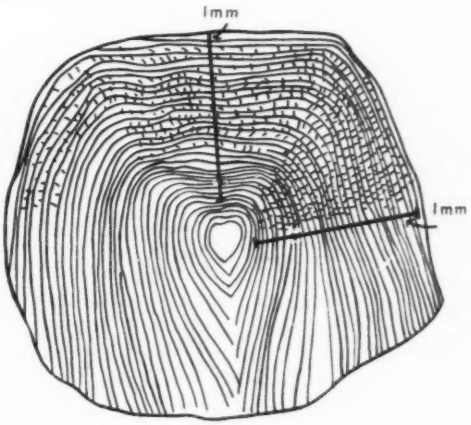
Type locality.—An outcrop in the Yaquina formation (upper Oligocene) of Zemorrian age from the southwest edge of the town of Waldport on the south side of Alsea Bay, first cut on U. S. Highway 101 south of Alsea Bridge. (H. E. Vokes, D. A Myers collectors).

Referred material.—Numerous scales of evidently the same species were found in outcrops of the Toledo formation in the Yaquina Bay area, Oregon. (Pl. 3, fig. 1–2).

Description.—Apical pole somewhat flattened with an indication of dorso- and basoapical corners. Circuli in apical pole concentric, very fine, about 25–26 in 1 mm. distance apicobasad across apical pole re-



TEXT-FIG. 2—*Paleobathygadus oligocenicus*, n. sp. Holotype, from the Fred Jasper Oil Co. well No. 1, at 4075 to 4101 ft. depth; 2 by 2.5 mm.



TEXT-FIG. 3—*Paleobathygadus yaquinensis*, n. sp. Holotype, from the Yaquina formation SW edge of town of Waldport on south side of Alsea Bay; 2.3 by 2.67 mm.

gion. Apical circuli distinctly folded, showing at least two folds. Nucleus small, pear shaped, approaching basal border. Few (about six or seven circuli meeting in acute angles in central basal axis. Ventral and dorsal basal circuli meeting asymmetrically in center due to a small microfold in the scale. Intercircular spaces widening very little towards basal pole, 23 circuli in 1 mm. across basal region of type. Those central basal circuli that do not meet in the midaxis with those from the opposite side, diagonally directed towards basal border, their ends rounded towards center. External circuli directed almost vertically towards basal border, extreme outermost circuli directed towards dorsal and ventral borders respectively. Checkerboard pattern of apical pole not very distinct in holotype since only a mold of coarse scale side is preserved whereas pattern is generally more distinct on smooth side.

Species distinguished by its moderately small size, fairly fine circuli, nucleus approaching basal border, flattened apical pole, and pattern of basal circuli.

The holotype of the species occurs at a locality in Alsea Bay, Oregon, which yielded a rich fish fauna that is characterized as follows: the lower Saucesian-Zemorrian species of *Etringus* is abundant and well preserved; several species of "*Beryx*" related to *Beryx sanjoaquinensis* David and *Beryx eogenus* David, respectively, (the upper Eogene and Zemorrian species of the genus in California, David, 1946) are fairly abundant; a small rattail scale and several large-scaled rattails are abundant; a shark's tooth, probably of the genus *Galeocerdo* is found; a rockcod-like (*Sebastodes*) scale and a sciaenid form are rare; several scales of *Paleobathygadus*, the genus under consideration, are found; undetermined bones and vertebrae occur abundantly. The fauna indicates considerable depth by the abundant presence of several species of macrurid fishes of two species or more of "*Beryx*," and of *P. yaquinensis*. All of these are restricted to deep water in Tertiary deposits. *Etringus*, the most abundant form in strata of this age, is always present. As in living genera of round herrings, scales of *Etringus* are evidently easily shed and the fish lived in large schools. This fact undoubtedly accounts for the great abundance of this genus in fossil deposits. The scales presumably drifted down the edge of the coastal slope, following certain currents, to be deposited in nearby deeper water. The remaining forms mentioned are rare and occur only as one or two scales. A bathyal environment is suggested by this fauna, possibly in a deep basin that was not far removed from shore. The strata are of Zemorrian age. "*Beryx*" does not range higher in the section. The Zemorrian on the other hand presents the basal beds of occurrence of *Etringus*.

In the section of the Toledo formation the following species occur with *P. yaquinensis*: Two species of "*Beryx*," similar to the ones mentioned above, macrurids, the usual round herring *Etringus*, and a genus of herring (undescribed), *Lampanyctus* sp., rare *Sebastodes* and *Seriola*-like fishes. *Beryx* and *Lampanyctus* (lanternfish), and the macrurids incidate bathyal or quite deep neritic environment, *Seriola* pelagic-neritic environment. Taking the presence of the abundant *Paleobathygadus* into account, we may conclude that the assemblage was deposited in a bathyal environment. The strata are of Zemorrian age.

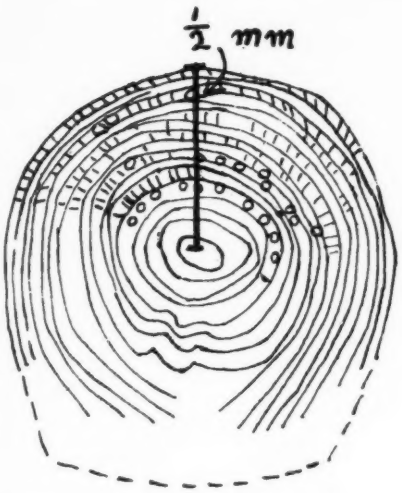
PALEOBATHYGADUS CAREAGRUS, n. sp.
Text-fig. 4

Holotype.—CIT 10448; 1.1 by 1.1 mm.

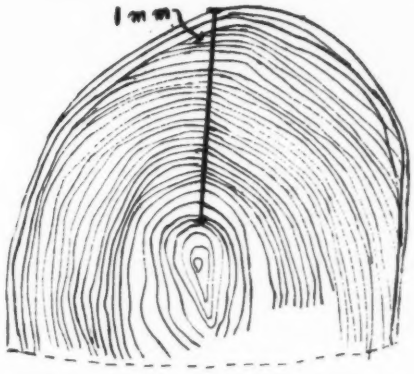
Type locality.—The Texas Oil Company well Careagra No. 1 at 1427–47 ft. depth. The well is located in Sec. 36, T. 5 N., R. 31 W., San Bernardino B. & M., Santa Barara Co.

Paratypes.—CIT 10449–10450; 1.2 by 1.33 mm. from the same locality.

Description.—Apical border and circuli completely rounded, concentric; circuli coarse, considering the small size of the species; intercircular spaces somewhat widening towards basal pole, 8 to 9 in 0.3 mm. apicobasad across spical pole as compared to 6 to 7 dorsoventrad across basal region. Checkerboard pattern of apical region very distinct in one of the paratypes where smooth side of scale is preserved. Pattern not quite as distinct in type. The fine transverse lines of the pattern narrowly approaching each other, round rather large indentations scattered over the central portion of the apical region. Nucleus almost central, rounded or nearly so, central two



TEXT-FIG. 4—*Paleobathygadus careagrus*, n. sp. Holotype, from the Texas Co. well Careagra No. 1, at 1427 to 47 ft. depth; 1.1 by 1.1 mm.



TEXT-FIG. 5—*Paleobathygadus zemorrianus*, n. sp. Holotype, from the Richfield Oil Corp. well KCL No. 1 at 1427 to 47 ft. depth; 1.67 by 1.9 mm.

or three circuli forming complete circles, those surrounding these externally either forming an acute angle towards basal mid-axis or, in the basalmost region, forming a zigzag pattern of one to three angles. External basal circuli diagonally directed towards central portion of basal border. Basal circuli successively shortening towards external borders, only the central ones reaching basal tip, giving the basal border a rounded to tapering appearance.

This species resembles *P. oligocenicus* with its rounded shape, the central nucleus, the distinct checkerboard pattern, and the comparatively coarse circuli, but the smallness of the scales and the apical pattern distinguish it.

The scale occurs in an assemblage uniting pelagic forms, which include a large undescribed clupeid genus, and a *Caranx*-like species, with deep-water forms represented by several species of rattails. A varied neritic fauna is absent. An assemblage of this combination could have been deposited only in deep-water of at least bathyal depth.

PALEOBATHYGADUS ZEMORRIANUS, n. sp.
Text-fig. 5

Holotype.—CIT 10437; 1.67 by 1.9 mm.

Type locality.—Richfield Oil Corporation well KCL No. 1, located in Sec. 1, T. 11 N., R. 20 W., San Bernardino B. & M., Kern Co., California, at 6452 ft. depth.

Description.—Apical pole of scale asymmetrical being a little higher towards dorsal side, due, no doubt to preservation; apical pole rounded without indication of folds or angles. Circuli concentric with apical border and very fine, 34–36 in 1 mm. distance basad from center of apical border. Nucleus very small and pear shaped, three times as much removed from apical border than from basal one; circuli surrounding nucleus forming elongate triangles lengthening rapidly towards basal region, three or four circuli forming acute angles in basal mid-axis. Intercircular spaces not widening noticeably towards basal border, about 30 circuli in 1 mm. distance across basal pole in dorsoventral direction. Basal circuli closest of those encircling nucleus, rounded, turning diagonally towards center of basal border, some of the most external ones directed dorsally. Checkerboard pattern not distinguishable.

The species is recorded as fairly abundant at the locality but the type seems to be the only reliable specimen preserved. The species is distinguished by its smallness and the fineness of the circuli, which are very numerous for the size of the scale; the nucleus is closer to the basal border than in any other species of the genus; the apical pole is rounded without indication of angulation. The absence of the checkerboard pattern may indicate that this species does not belong to this genus, but this is more likely caused by the type of preservation.

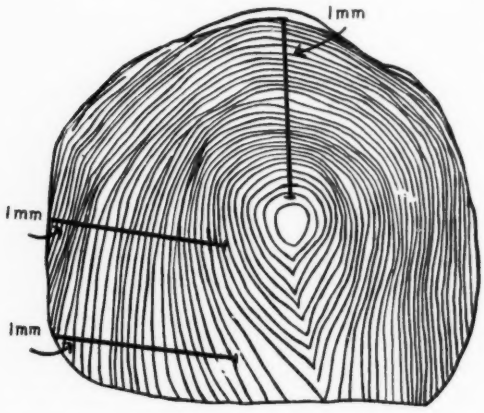
In this facies of the well, *P. zemorrianus* occurs with *Beryx kcli* David, a *Macrurus*-like form, *Etringus*, and a jack (*Caranx?*). A bathyal assemblage very similar to the one observed for *P. yaquinensis* from Alsea Bay in Oregon, is indicated. The strata are of Zemorrian age.

PALEOBATHYGADUS WILMINGTONENSIS, n. sp.
Text-fig. 6

Holotype.—CIT 10438; 2.1 by 2.4 mm.

Type locality.—General Petroleum Oil Company well Terminal No. 1, Sec. 4, T. 5 S., R. 13 W., San Bernardino B. & M., at 5258–5276 ft. depth, Wilmington Field, Los Angeles Co., California.

Description.—Apical pole of the small scale fairly well rounded with faint indications of dorso- and ventroapical corners. Apical circuli concentric with apical border, very fine, about 30 in 1 mm. distance basad from center of apical border. Nucleus approaching basal border slightly, rounded to pear shaped, surrounded by evenly spaced circuli, about 10 of these meeting in acute angles in the basal midaxis; axis slightly asymmetric, directed towards dorsal side. Circuli closest to those that end in basal midaxis rounded and meeting basal border diagonally; more external ones directed vertically to the basal border. Intercircular spaces widening a little towards basal pole. About 29 circuli in 1 mm. distance dorsal from ventral border at level of nucleus, about 19–20 in that distance close to the basal border. Checkerboard pattern visible in places, but faintly so. Only central basal portion of coarse side of scale preserved, the remaining portion shown by an imprint of smooth side, still showing the circuli fairly clearly.



TEXT-FIG. 6—*Paleobathygadus wilmingtonensis*, n. sp. Holotype, from the General Petroleum Oil Co. well Terminal No. 1, at 5258 to 5276 ft. depth; 2.1 by 2.4 mm.

The scale shows the typical pattern of the genus. Its is somewhat similar to *P. yaquinensis*, but distinguished from that species by its rounded shape, the finer circuli with smaller intercircular spaces, and a slight difference in the basal pattern.

The facies where this species occurs unites a rich assemblage of piscine forms of the following types: The bathypelagic forms *Lampanyctus* (lanternfish), *Cyclothone*, and *Myctophum* are very abundant throughout, as scales and as skeletons; pelagic forms of deeper water such as *Bathylagus* and *Chauliodus* (viperfish), are represented. Neritic pelagic forms such as *Xyne grex*, *Ganolytes* (an extinct shadlike form), occur; neritic forms such as *Lompoquia* and a mackerel are fairly abundant. The pelagic *Syngnathus* (pipefish) is abundant in places; and *Thyrsocles*, a near-shore deep-water fish is present. The great abundance of the bathypelagic forms, especially as skeletons, and occasional appearance of forms like the viperfish and *Bathylagus* clearly indicate an environment over very deep water. The neritic forms were carried to this zone sinking down the slope, the pelagic and bathypelagic forms slowly sank down to the bottom. The facies most likely represents a deep basin, close to the bottom of the slope, not too far removed from the shore. The strata are of uppermost Mohnian age.

Genus PROBATHYGADUS, n. gen.

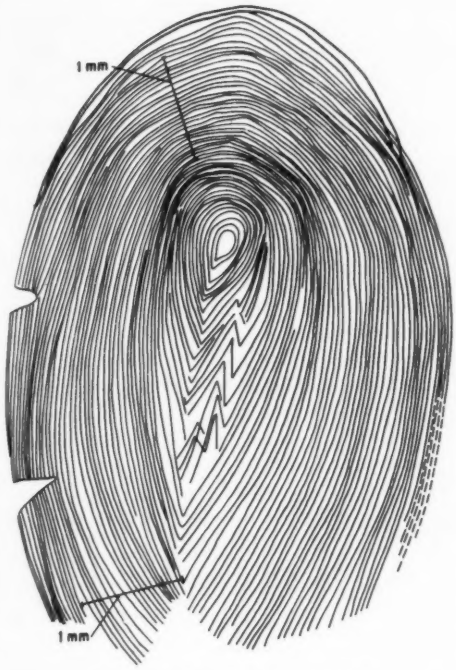
Type species.—*Probathygadus keaseyensis* David, n. sp.

The scales of this genus seem close to that of the Recent genus *Bathygadus*, they are distinguished by the finer and more numerous circuli and by the rounded basal border; the external basal circuli extend further towards the center of the basal border and almost meet in the midaxis.

PROBATHYGADUS KEASEYENSIS, n. sp.
Text-fig. 7

Holotype.—CIT 10451; 6 by 4.3 mm.

Type locality.—An outcrop of the Keasey



TEXT-FIG. 7—*Probathygadus keaseyensis*, n. sp. Holotype, from the Keasey formation at an outcrop ca. 3000 ft. S of Mist, Keasey Quadrangle, N.W. Oregon; 6 by 4.3 mm.

formation, ca. 3000 ft. S. of Mist, Keasey quadrangle, northwest Oregon (Vokes, Durham, Myers collectors).

Paratype.—CIT 10452, a fragment showing central portion of scale, 3 by 2.5 mm. from the same locality.

Description.—Holotype showing well preserved mold of a scale rather large for the group, outstanding in the many closely spaced circuli. Smooth side of scale preserved in a small triangle of apical region. Coarse side of scale complete but slightly distorted by a "microfault" in basal region. Apical circuli rounded, forming a vaguely acute angle in midaxis. Transverse lines and checkerboard pattern of apical pole region very indistinct, visible in preserved portion of smooth side only. Pattern suggested only by very fine closely set transverse lines. Nucleus much closer to apical border than to basal; distance nucleus to apical border, one third of length of scale. Widening of intercircular spaces towards basal border, not very pronounced; about 23 circuli in 1 mm. basiapicad across the apical region as compared to about 17 across 1 mm. of basal region in ventrodorsal direction. About 20 to 24 basal circuli forming an acute angle in basal midaxis (the exact number can not be counted since the tip of the basal region is disturbed by a microfold of the matrix). Some of the central basal circuli forming an irregular pattern of zigzag angulation; external basal circuli concentrically rounded towards basal border.

This scale is distinguished by its large size, its length being distinctly greater than its depth; the very fine circuli; and the rounding of the basal circuli towards the basal center.

The fish fauna from the type locality of this species is characterized as follows: Fragments of *Wisslerius* David, a herring, occur; several species of *Beryx* are present, which differ somewhat from the two species known from the Upper Eogene of California (David, 1946). Two species of macrurids and a lanternfish, *Lampanyctus* sp., are common. A merluccid form (hake), a percomorph fish, an *Iniomus*-like form, a serranid (grouper), and a small species of macrurid are less common or rare. The fauna indicates considerable depth. A bathyal aspect is suggested by the presence of "*Beryx*," *Lampanyctus*, ?*Iniomus*, the three species of macrurids, and the bathygadid described here; all these forms are restricted to deep water. *Wisslerius* at this locality is always fragmented, and its scales had probably been carried away from some distant locality in shallower water before being deposited here. Hakes also occur pelagically over deep water or in deep water in the winter; the remaining forms, serranid and percomorph are quite rare. The strata are likely to be of Refugian age; macrurids are present and abundant and the basal beds of their occurrence seem to be in the Refugian; on the other hand such forms as *Wisslerius* and the ?*Iniomus* have their uppermost occurrence in the Refugian also.

Family GADIDAE
Pl. 69, fig. 5–9; Pl. 70, fig. 1–3

The scales of the cods and hakes are well known; the genera *Gadus* and *Microgadus* etc. have typically rounded to oval scales with concentric circuli and very distinct transverse radiations. They are very different from the "deep-sea cods." Cockerell

(1911, p. 212) distinguishes the Gadinae and Brosminae from the Merlucciidae and Phycinae, which have more or less angled circuli and no radii. He states:

> according to the scales some type allied to the Macrouridae may have given rise to the different lines represented by *Merluccius, Urophycis* and *Enchelyopus*, but the Gadinae with the Brosminae must have another origin, although no doubt all can be referred to a common ancestor by going back far enough.

In connection with the present report, a variety of Phycinae were studied, such as *Urophycis chesteri* Goode & Bean, *Urophycis chuss* Walbaum, *Antimora viola* Goode & Bean, *Physiculus japonicus* Hilgendorf, *Lepidion insosima* Günther, *Lotella phycis* Temminck & Schlegel. Peabody (1931) describes *Urophycis regius* (Walbaum) and *Physiculus nigrescens* Smith & Radcliffe; Cockerell (1912) pictures *Urophycis regius* (Walbaum). The scales of the deep-sea cods (Phycinae) are distinguished readily from other gadid forms by the marked distinction between the patterns of apical and basal poles: the apical circuli are rounded and usually concentric; the basal circuli directed vertically to the basal border and usually parallel to each other. In the true cods the circuli are rounded and concentric throughout with little differences between apical and basal poles. The apical pole of the Phycinae is quite often weak and shows an irregular border; the apical circuli may be very irregularly angled (*Lotella phycis*, Pl. 70, fig. 2, *Physiculus japonicus*, Pl. 70, fig. 1); the apical circuli may be acutely angled with intercircular spaces progressively widening towards the apex of the apical midaxis, while the more external circuli proceed at oblique angles towards the apical margin (*Urophycis chuss*, Pl. 1, fig. 9); the apical pole may be deeply furrowed extending into a projection at each side apically beyond the furrow (*Phycis chesteri*, Pl. 1, fig. 5, 6). The nucleus of the Phycinae most often approaches the apical border and is oblong. The more or less vertical basal circuli approach the basal border obliquely; in distinction to *Bathygadus* the phycin basal circuli seldom form irregular acute angles in the midaxis, or if they do, the angles are extremely elongated, pointed, and only a very small number of such angles is formed (*Lotella phycis*). The basal midaxial region of the Phycinae may be entirely free of circuli (*Urophycis*); the median basal circuli may be parallel (*Phycis chesteri*); or, these circuli may be entirely irregular, some meeting in the center, others ending blindly, others forming an irregular angular pattern; the angles are not always concentric to each other (*Physiculus japonicus*).

Genus ECLIPES Jordan & Gilbert

This extinct gadid genus was described by Jordan & Gilbert from skeletal remains. It is represented in California in Miocene strata in moderate abundance was reviewed in David, 1943 (pp. 19–22). Four species are known so far: *E. veternus* Jordan & Gilbert, *E. extensus* Jordan, and *E. santamonicae* David from southern California, and *E. manni* Jordan from Lompoc, California.

Genus PROGADUS [?ECLIPES], n. gen.

Type species.—Progadus pliocenicus n. sp.

The scales described here may very well be the scales of *Eclipes*, specimens of that genus having always been found in a state of preservation completely deprived of scales. As do the skeletal remains referred to *Eclipes*, the scales show gadid characteristics, but no definite relationship to any Recent genus can be established.

Description.—The apical portion of the scale evidently was weak, it is rarely preserved, while central and basal portions are well preserved and quite compact. Lateral circuli more or less vertical from apical to basal border. Median apical circuli either forming one definite angle in midaxis with intercircular spaces widening towards apex, or median circuli forming two apici, divided by a rather deep pronounced fold; extreme apical portion of scales of the latter type lost most often, leaving some indication that two apical projections were present similar to those found in some Recent gadid genera. Nucleus usually oblong. Intercircular spaces distinctly widening towards basal pole; lateral basal circuli vertical or obliquely directed outward towards rounded basal border; median basal circuli irregular; some forming a few elongate angles in midaxis; others ending blindly or forming an irregular zigzag pattern.

Thus the genus shows characteristics found in various Recent gadid genera: The apical pole shows some resemblance to *Phycis chesteri* which has scales of two types, some with two apical projections, others showing only one angle, pointed in the midaxis. A weak apical pole with an indistinct circular pattern, as shown by some *Progadus* scales, is found in *Physiculus japonicus* and *Lotella phycis*. The nucleus of *Progadus* is oblong as found in *Physiculus* and *Lotella*. The basal pattern also resembles these two genera more than any others studied, in the irregularity of the median basal circuli which are not divided in the center by a space free of circuli, and in the vertical lateral basal circuli; in *Progadus* however the basal pattern is not as irregular as in the two Recent genera and the circuli are more concentrically arranged. *Bathygadus* scales present irregular median basal circuli with zigzag pattern much like the one shown by the fossil form, but in *Progadus* the circuli never form regular concentric pointed angles in the midaxis of the basal region as they always do in *Bathygadus*. The scales of *Progadus* also lack the checkerboard pattern and the rounded apical region characteristic of *Bathygadus*.

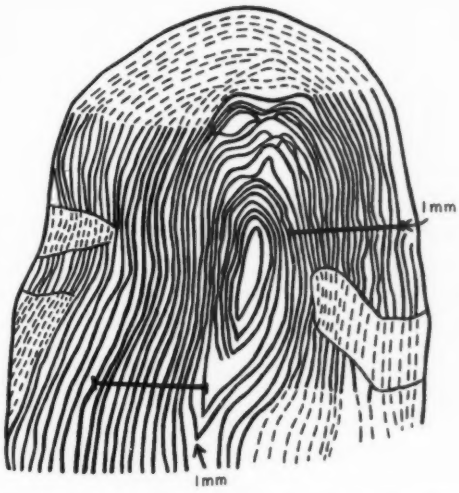
PROGADUS PLIOCENICUS, n. sp.
Pl. 71, fig. 3–5; Text-fig. 8

Holotype.—CIT 10453; 4 by 3.67 mm.

Type locality.—Oxnard Oil Company well Vanoni No. 1, Ventura Co., Sec. 10, T. 1 N., R. 21 W., San Bernardino B. & M., at 5048 ft. depth.

Paratypes.—One specimen, unnumbered, presents a small portion of the central part of a poorly preserved scale. The scales shown on Pl. 3, fig. 3–5, are from the same well, all three are preserved in the collection of the Richfield Oil Corporation Paleontology Laboratory, Long Beach, California, as the company's type No. 18.

Description.—Apical border of type and of one of the other specimens incomplete, evidently was weak (Text-fig. 8; Pl. 71, fig. 5). Where preserved, median apical circuli show an irregular pattern: in one scale circuli concentrically arranged forming a distinct median pointed angle (Pl. 71, fig. 3); in another scale two apices are distinct, each forming a pointed angle in apical border,



TEXT-FIG. 8—*Progadus pliocenicus*, n. sp. Holotype, from the Oxnard Oil Co. well Vanoni No. 1, at 5048 to 65 ft. depth; preserved portion 4 by 3.67 mm.

apical circuli concentrically following these angles (Pl. 71, fig. 4). Lateral apical circuli in all specimens running vertically from apical to basal borders, their apical ends may be rounded towards median axis of pole. Nucleus more or less central, oblong. Basal circuli vertical, directed straight towards basal border, or with externalmost circuli bending outwards toward dorsal or ventral corners; intercircular spaces widening toward basal border. Innermost basal circuli meeting in two or three very elongate pointed angles, or ending abruptly before reaching basal border.

The basal pattern shows the most marked difference between this and the following species. *P. pliocenicus* does not show the very marked zigzag pattern in the basal extremity; intercircular spaces are widening more gradually in *P. pliocenicus* and the width between apical and basal circuli is not so distinctly different as in *P. miocenicus*.

Scales of this species were found in Pliocene strata of the Ventura Basin. In these strata fish remains are very rare generally, and this occurrence of scales is very local and restricted. The assemblage includes *Merluccius*, bones and vertebrae. This combination of piscine remains may have represented the remains of a bottom fauna in deep neritic or bathyal surroundings. Gadid-

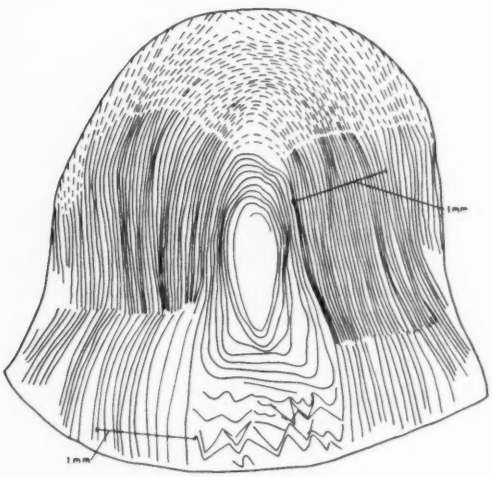
dominated bottom faunas seem to exist in the Recent sea in temperate waters north of Cape Hatteras. In the Pliocene strata of the Los Angeles Basin scales are even rarer, than in the Ventura Basins.

PROGADUS MIOCENICUS, n. sp.
Pl. 71, fig. 6; Text-fig. 9

Holotype.—The type is contained in the collection of the Richfield Oil Corporation Paleontology Laboratory, Long Beach, California, as their type No. 13. Preserved portion of scale 4 by 4.67 mm., length of complete scale estimated at 5.33 mm.

Type locality.—Richfield Oil Corporation well Guernsey No. 1, Sec. 2, T. 5 S., R. 13 W., San Bernardino B. & M. at 5144–52 ft. depth. Wilmington area of Los Angeles Basin; upper Miocene strata.

Description.—Scale rather large, major portion of type remarkably well preserved, only extreme portion of apical pole missing. Apical pole, where preserved, showing rather fine lateral circuli, definitely rounded in direction of apical midaxis. (Pl. 71, fig. 6; Text-fig. 9). Central apical circuli coarse, concentric, widening towards their apex and forming very obtuse asymmetric angles with the apical border; very slightly curved into a furrow. Intercircular spaces in apex very distinctly widening. Nucleus oblong, elongated apicobasad; surrounded by four to five completely closed concentric circuli. Elongately pear shaped these "nuclear" circuli approach each other closely laterally to nucleus, becoming coarser apicad and basad to nucleus with much wider intercircular spaces. Lateral circuli directed vertically from apical to basal border, fine and closely approaching each other. Two-thirds apicobasad from apical border circuli turning abruptly outwards towards lateral (dorsal and ventral) borders of scale. Intercircular spaces widening considerably towards basal border; 23–25 circuli in 1 mm. distance in ventrodorsal direction from apical end of nucleus; about 10 circuli in 1 mm. distance in extreme basal portion of scale. Central basal circuli rather coarse, intercircular spaces widening, about four or five basal central circuli (immediately external to those surrounding the nucleus) forming acute angles; these completely asymmetrical, pointing dorsad from central midaxis. Circuli of central portion of basal pole beyond these angled circuli forming a completely different variegated zigzag pattern. This section probably comprising an increase of growth during a number of years; 5 or 6 irregular, indistinctly overlapping wavelines following each other, each forming a number of irregular acute angles in varied directions; the angles are not necessarily connected to each other. Dorso- and ventrobasal scale angles rounded; here the circuli are rather wide and directed diagonally towards dorsal and ventral borders, respectively. The basal zigzag pattern of this species distinguishes it clearly from *P. pliocenicus*, the only other species of the genus.



TEXT-FIG. 9—*Progadus miocenicus*, n. sp. Holotype, from the Richfield Oil Corp. well Guernsey No. 1; preserved portion 4 by 4.67 mm., length of complete scale estimated to be 5.33 mm. Dashed lines indicate restored portion.

In this facies of the well a varied assemblage occurs: Complete skeletons of bathyal or bathypelagic forms are very abundant throughout, such as *Cyclothone*, *Bathylagus*, *Lampanyctus*. Scales of *Lampanyctus*, *Myctophum* and fragments of skeletons of *Chauliodus* occur in places. Pelagic forms as *Scomberesox*, "*Sarda*," and Carangids occur; *Thyrsocles*, a near-shore deep-water form is present. Of neritic forms, *Xyne grex* is abundant, *Ganolytes* to a lesser degree, *Lompoquia* and a mackerel are fairly common. The great abundance of bathyal and bathypelagic forms, represented by skele-

tons and scales, does not leave much doubt that the assemblage was accumulated in deep water beyond the neritic zone. Burial may have occurred in a deep basin near the bottom of the coastal slope whereto the neritic forms drifted down the slope. A very similar assemblage is described above for the General Petroleum Company well Terminal No. 1. The great abundance of bathypelagic forms in both assemblages is remarkable.

Family MACRURIDAE
Pl. 70, fig. 5–8

Scales of the family were described and figured by Cockerell (1912, 1913) and Peabody (1931). Macrurid scales are outstanding in two ways: on the one hand they all follow a common basic pattern that allows their immediate recognition as members of the family; on the other hand they show such multitudes of variations of this pattern that species determinations are easily made. Actually Macruridae are one of the few families in which scale descriptions have been given to a greater extent for use in species designation (Garman, 1899; Smith & Radcliffe 1912; Weber, 1913; Gilbert & Hubbs, 1916, 1920; Parr, 1946). The scales of the multitude of living species have not been studied sufficiently to allow recognition of generic patterns. Only Parr (1946) presents illustrations that make comparisons of scales of different genera possible; further studies of this type may lead to recognition of generic scale patterns. Parr's paper is restricted to North Atlantic and middle American seas; his studies clearly indicate that many of the species from other parts of the world are not yet definitely classified as to genera. While a differentiation into specialized patterns is obviously present in some genera, other more primitive patterns may occur in several genera. All fossil scales of the macrurid type have been classified under the somewhat outdated family name Macruridae. To classify the fossil scales definitely into one of the subfamilies that have been proposed by modern authors does not seem advisable at this time. An exception are the Bathygadidae which are also considered as a subfamily of the Macruridae by some students of the Recent families. Scales of Bathygadidae and Macruridae are so different that they have been considered here as two separate families.

The basic pattern of the family is well shown by *Macrurus anguliceps* Garman (Pl. 70, fig. 5). The nucleus is almost central. The circuli are concentric and extend around the whole scale. The apical spines, if thickly set, or the apical pigmentation may prevent visibility of the circuli in that region. The circuli characteristically are sharply angled in the midbasal axis and in diagonal lines extending from the nucleus to the basodorsal and basoventral corners; in the apical region the circuli are more widely angled. The dorsalmost and ventralmost circuli may end diagonally towards the respective margin without extending all around the basal pole. The apical pole is beset with spines; in the basic pattern these are arranged in rows in straight apical direction or diagonally inclined towards the midapical axis.

Various progressive deviations from this basic pattern can be observed. The angulations of the basal circuli may be asymmetrical; the circuli may form additional concentric angles, as in *Coryphaenoides cinereus* Gilbert (Pl. 70, fig. 6) or the angles may become progressively vague, as in *Coelorhynchus argentatus* Smith & Radcliffe (Pl. 70, fig. 7), until the circuli have an almost rounded appearance, as in *Malacosephalus laevis* Lowe (Pl. 70, fig. 8), even though the original pattern is still recognizable. The apical circuli may be divided by the rows of spines into series of parallel groups, the circuli being interrupted in their course whenever they cross a spine, their direction being slightly deviated at the other side of the spine. The scales vary in size and coarseness, and the circuli may be fine or coarse, densely spaced or with wide intercircular spaces. The spines may show all possible variations in length, in thickness, in shape, and in pattern: they may form rows, may be arranged in imbricate fashion, or be entirely irregular; they may be densely to sparsely set covering the pole; or, the spines of the rows may be fused, forming a ridge. All spines may be pointed or only the marginal ones, the others being more or less rod shaped. The spines may be divided into two or more groups. They may have very wide bases, as in *Coelorhynchus argentatus* Smith & Radcliffe (Pl. 70, fig. 7). Numerous ex-

amples of these variations have been illustrated by the various authors. Scales in the extremities of the body, extreme tail end, head, extreme dorsal or ventral side, become more and more asymmetrical and should not be used for identification. In these the number of apical rows of spines and grooves becomes smaller, the scale more elongate, longer rather than deep, and the shape becomes more and more irregular. The complete difference of the head scales has been well demonstrated by Parr (1946). No head scales were found in the fossil materials. One reason why macrurid scales are so abundantly found in fossil deposits may be that they are easily shed. The scales of the head are likely to be retained on the skeleton in most cases.

Bolbocara gyrinus Jordan

Bolbocara gyrinus Jordan, 1927, Stanford Univ. Pub., Biol. Sci., vol. 5, no. 2, p. 10–11.

The type specimen is still the only known representative of the genus and the only specimen yet recovered that shows at least the major portion of a fossil macrurid skeleton in this region.

Genus Promacrurus, n. gen.

Type species.—Promacrurus zemorrianus, n. sp.

A number of species have been united in this genus that have scales more closely resembling the primitive pattern of the family and that do not show any specialization distinctive enough to allow generic differentiation.

The scales of *Promacrurus* are much deeper than long in the large scaled species, to almost rounded in smaller scaled forms. The circuli are concentric and show characteristically three angles in the basal region, one in the midaxis, one each in the diagonals from the nucleus to the dorso- or ventrobasal corners of the scale. The nucleus is central or closer to the basal border. The apical spines form linear subparallel to slightly diverging rows; the central row or rows are longest and present the greatest number of spines. The spines of neighbouring rows are usually placed in an imbricated pattern; the spines are fairly strong and rigid, closely applied to the scale; those protruding beyond the apical border are stouter and conical, the others rod shaped.

Compared to the scale patterns shown by Parr, the scales assigned to *Promacrurus* seem to come closest to *Chalinura* Goode & Bean. *P. zemorrianus*, *P. oregonensis* and *P. newmanni* are closely related to each other and form by far the most abundant species in the California and Oregon Zemorrian and the California Saucesian, respectively. *P. alseanus* and *alferitzi* are coarser forms; *P. mimus*, *P. saucesianus* and *P. asymmetricus* represent species with small or degenerate scales.

Promacrurus zemorrianus, n. sp.
Text-fig. 10

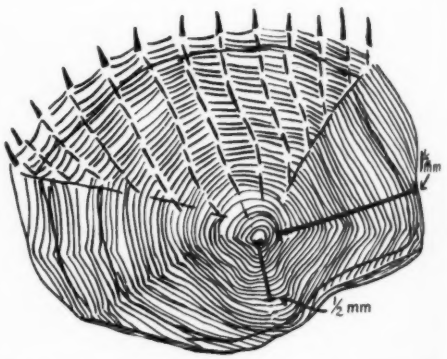
David, 1944, Carnegie Inst. Washington, Pub. 551, no. 3, pl. 2, fig. 18, 18a.

Holotype.—CIT 10454; 3+0.3 by 3.7 mm.

Type locality.—The Texas Company well Pioneer Unit Plan No. 1 at 6558 ft. depth; the well is situated in Sec. 33, T. 11 S., R. 23 W., San Bernardino B. & M., San Joaquin Valley, Sunset District, California.

Paratypes.—Eight specimens chosen from a multitude of specimens from the same well at depth 6228–6622 ft. are preserved as CIT 10455–10462; these range in size (mm.): 2.4 by 2; 3+0.33 by 3; 3.2 by 3.4; 3.8 by 3.3; 3+? by 4; 3.67+0.2 by 4.33; 4.3+? by 4.3; 4+? by 4.33 mm.

Description.—Typical scales from sides of body rectangular with rounded corners, deeper than long. Apical and basal circuli of this fairly coarse species concentric and continuous. Basal circuli forming sharp to



Text-Fig. 10—*Promacrurus zemorrianus*, n. sp. Holotype from the Texas Co. well Pioneer Unit Plan No. 1, at 6547 ft. depth; 3+0.3 (length of spine) by 3.7 mm.

rounded angles in the basal midaxis or in close vicinity of axis and sharply pointed angles in the laterobasal diagonals; in addition a more or less accentuated angle may be formed between laterobasal angles and apical pole area. Nucleus approaching basal border and usually found at a distance of two-fifths of length of scale anterior to basal border. Circuli coarse, intercircular spaces small. Circuli approaching each other closest near nucleus; intercircular spaces widening laterally towards dorsal and ventral borders, about 28 to 29 in 1 mm. distance ventrad from dorsal border of average sized scale, 19 to 20 in larger scales. Circuli in apical pole continuing concentrically with each other and apical border; interrupted by each row of spines to continue in a slightly changed direction; intercircular spaces in apical region fairly wide, 16 to 19 in 1 mm. distance basad from apical border. Apical circuli slanting in the direction of the midaxis, forming an obtuse angle in midaxis divided by central row of spines. Typical lateral scales with 13 to 15 rows of spines, up to 16 in large scales, and any lower number, 6, 8, 11 in asymmetrical atypical scales coming from extremities of fish body. Spines closely applied to scale forming linear subparallel rows, very little diverging from central row; those protruding the apical border conical; the others rod shaped, their apical ends bordering the basal portion of the succeeding spine. Spines set along fairly sharp ridges, forming rims of the apical folds and extending towards nucleus. Numbers of spines in various rows decreasing from maximal number in central row to 1 or 2 in end rows. Numbers of spines found in some typical scales were as follows:

Numbers of spines in:			Total no. of rows
Ventral rows	Central row	Dorsal rows	
1,3,6,7,8,9,	10	8,7,7,5,2,1	13
1,3,4,6,8,9,11,11	13	10,10,8,7,5,4,2	16
1,3,5,6,7,9	10	8,7,6,4,3,2,1	14
2,5,6,7,8,9	13	12,11,10,8,6,3,2,1	15
1,2,4,5,6,7	8	7,6,5,3,1	12

This scale is characteristic for the middle Zemorrian of the Texas Pioneer Unit Plan well. If cores of increasing depth are investigated from this well, the scale becomes more and more abundant in the lower middle Zemorrian and is dominant in this part of the section. In large parts of the section only various species of macrurids were found with exclusion of other piscine material; the sea in these horizons was undoubtedly very deep, 1,000 fathoms or more, and most likely of abyssal nature. *Etringus* where it appears is highly fragmented. (For details on this fauna see David, 1944, p. 32–33.) *P. zemorrianus* is found in the Zemorrian section of many parts of California; it characterizes strata of that age and is the most abundant rattail found in California. Its latest occurrence is the Saucesian.

PROMACRURUS OREGONENSIS, n. sp.
Text-fig. 11

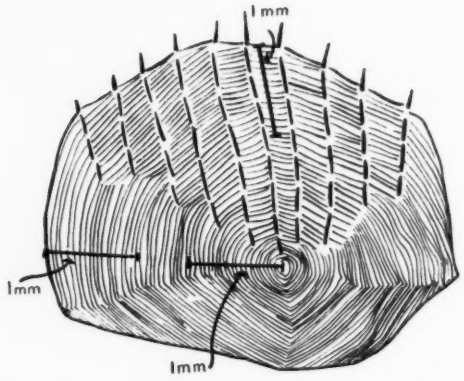
Holotype.—CIT 10463; 3.67 by 4.67 mm.

Type locality.—Yaquina formation, southwest edge of town of Waldport on south side of Alsea Bay, first cut on U. S. 101 south of Alsea Bay bridge.

Paratypes.—A specimen (CIT 10464) from the same locality shows the spines protruding beyond the apical border well preserved; it measures 3+0.33 by 3.33 mm. Seven additional specimens from the same locality, CIT 10465–10471 measure (mm.); 3.33 by 4.67; 3.1 by 4.6; 3.4+0.33 by 4.1; 3.3 by 4.0; 3.3 by 3.8; 3.0+0.33 by 3.2; 2.2+0.17 by 3.17. Smaller scales (unnumbered) measure 2.75 by 3.0; 2.75 by 2.5; 2.67 by 1.6 mm.

Referred material.—Five specimens from the Nye mudstone at the north shore of Yaquina Bay approximately 75 ft. above the base of the formation, CIT 10472–10476; 3.4 by 4.67; 3.9 by 4.67; 3.6 by 4; 3.3 by 3.2; 3.33 by 3.2 mm.

One fragmented specimen from the Keasey formation in northwest Oregon, ca. 3000 ft. south of Mist, Keasey Quadrangle, CIT 10477; 4.3 by 4.2 mm. Five other specimens from the same locality may be-



TEXT-FIG. *11*—*Promacrurus oregonensis*, n. sp. Holotype, from the Yaquina Formation S.W. edge of Town of Waldport on south side of Alsea Bay; 3.67 by 4.67 mm.

long to the same species but they do not appear as coarse as the other specimens listed above.

Description.—Typical lateral specimens rectangular and fairly coarse, deeper than long. Circuli continuous and concentric with periphery of scale. Basal circuli with sharp angles in laterobasal and midbasal diagonals; additional angles may be formed in some specimens. Circuli along basal border wavery, forming small folds, most often only on one side of midaxis. Circuli nearest to nucleus finest and approaching each other closely; about 21 central basal circuli found in 1 mm. distance; 16 to 19 in 1 mm. distance beginning at lateral borders. Nucleus surrounded by completely pear shaped circuli and located nearer to basal border: about two fifths of length of scale apicad to basal border. Apical circuli spaced wider, 14 to 16 in 1 mm. distance beginning at apical border, up to 19 in some. Apical circuli parallel, sloping upwards towards apical midaxis interrupted by rows of spines as in previous species. Typical grown specimens with 9 to 10 rows of spines placed on ridges protruding above coarse side of scale. In atypical scales from extremities of body number of spine rows decreasing according to amount of asymmetry of scale shape. Number of spines about 8 in central row of larger scales; their number decreasing progressively towards lateral (dorsal, ventral) borders of scale, similar to arrangement in previous species. Spines on body of scales rod shaped, those protruding beyond apical border pointed and up to 0.37 mm. long.

The scale is very similar and evidently closely related to the preceding species, *P. zemorrianus*. The circuli of *P. oregonensis* are not quite as coarse and the intercircular spaces smaller, the average number of rows of spines is distinctly less, 9 or 10 as compared to 13 to 15 in *P. zemorrianus*. The spines protruding beyond the apical border seem longer in *P. oregonensis*, 0.33 to 0.37 mm. in grown scales as compared to 0.3 or less in *P. zemorrianus*. The Oregon species is just as abundant in Zemorrian localities of Oregon as *P. zemorrianus* is in localities of same age in California. The scale occurs abundantly in deep-water deposits of bathyal to abyssal depth of Zemorrian age. The ecology of the type locality in Yaquina Bay was described above (see under *Paleobathygadus yaguinensis*). The species is quite abundant in the Nye mudstone of

---

EXPLANATION OF PLATE 69

FIG. *1*—*Bregmaceros atlanticus* Goode & Bean. Scale removed from USNM 116837, from Tortugas, Florida; collector W. H. Longley. ×22.5. (p. 570)

2—*Gadomus* [*?Bathygadus*] *longifilis* (Goode & Bean), from Station 2392 Albatross Expedition, at 734 fathoms. ×19.7. (p. 570)

3,4—*Bathygadus antrodes* Jordan & Gilbert, from Station 5083 Albatross Expedition. *3*, Lateral scale on antero-dorsal portion of fish. ×13. *4*, Another scale from same specimen ×19. (p. 570)

5,6—*Phycis chesteri* Goode & Bean, from off Cape Cod. *5*, Lateral scale below dorsal fin. ×12.4. *6*, Another scale from same specimen. ×10.3. (p. 575)

7,8—*Antimora viola* Goode & Bean, from off Delaware. *7*, Lateral scale below dorsal fin. ×8. Another scale from same specimen. ×15.5. (p. 575)

9—*Urophycis chuss* Hálbaum, from off Bar Harbor, Maine. ×10. (p. 575)

1

2

3

4

5

6

7

8

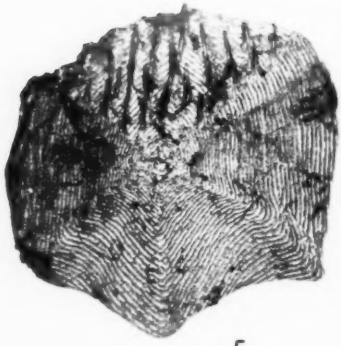
9

1

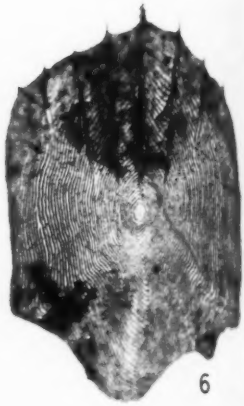
2

3

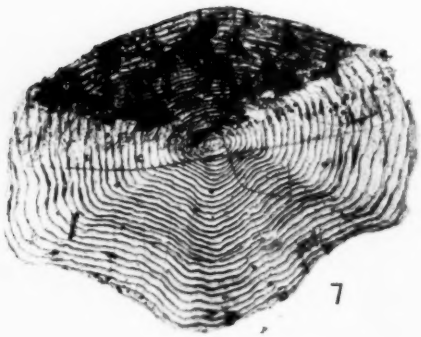
4



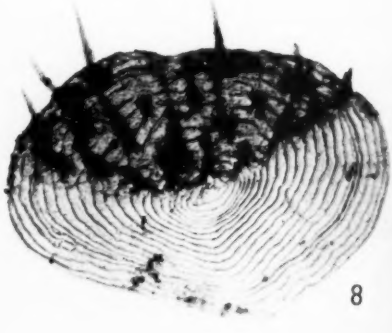
5



6



7



8

the Yaquina Bay. At this locality the Zemorrian *Etringus*, most often fragmented, and bone fragments are abundant with *P. oregonensis*. A species related to *Albula*, a ladyfish, occurs (one scale), and at least three species of macrurids are present, two of these are reasonably abundant. An *Albula*-like species is also known from a similar Zemorrian faunule in California (Texas Oil Co. well Careagra No. 1). The relative abundance of the rattails indicates a deep-water deposit. There is nothing else that permits a definite determination. *Etringus* fragments are abundant, but their state of preservation does not assure nearness to shore. *Albula* occurs pelagically, fairly close to shore. Age of this locality is either lower Saucesian or Zemorrian. Occurrence of this form in the Keasey formation, at a locality of bathyal ecology and Refugian age (see above, under *Probathygadus keaseyensis*) is not quite certain. The scales from this locality present a finer texture, and are mostly poorly preserved.

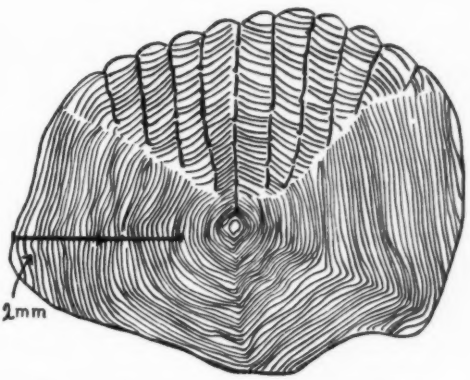
PROMACRURUS sp.

Scales similar to *P. oregonensis*, but smaller and rounded in shape were found together with this species at the Yaquina Bay locality. These probably present a different species, but none of the scales is sufficiently well preserved to warrant description of a species.

PROMACRURUS NEWMANI, n. sp.
Text-fig. 12

Holotype.—CIT 10497; 4.30+0.20 by 5.4 mm.

Type locality.—Texas Company well Newman No. 1, Sec. 23, T. 29 S., R. 28 E., San Bernardino B. & M., Kern River District, San Joaquin Valley, California, at 6177–6221 ft. depth.



TEXT-FIG. *12*—*Promacrurus newmani*, n. sp. Holotype, from the Texas Co. well Newman No. 1, at 6177 to 6221 ft. depth; 4.30+0.20 by 5.4 mm.

Paratypes.—CIT 10498–10500; 4.2+0.30 by 5 mm., 4.33+0.40 by 4 mm., 4 by 4.33 mm. from the same locality, same depth. CIT 10492–10493; 2.67 by 3 mm. 2.33 by 2.67 mm., from the same locality at 5741–5800 ft. depth.

Description.—Scale rectangular with apical pole rounded. Size moderately large. Basal circuli forming distinct sharp or rounded angles in midbasal axis and in diagonals from nucleus to basodorsal and ventral corners. Circuli in basal region often wavery, forming miniature folds. Basal circuli rather coarse, normally 18 to 21 in 1 mm. distance ventrad from dorsal border, varying however from 16 to 23 in extreme cases. Nucleus rounded, approximately two fifths of scale length apicad from basal border. Apical portion well differentiated from rest of scale; apical circuli widening, divided

---

EXPLANATION OF PLATE 70

FIG. *1*—*Physiculus japonicus* Hilgendorf, from off Myiako, Japan. ×14.6. (p. 575)
2—*Lotella phycis* Temminck & Schlegel, from off Sendai, Japan. ×23.3. (p. 575)
3—*Lepidion inosima* Gunther, from off Totami, Japan. ×24.9. (p. 575)
4—*Merluccius productus* (Ayres), from off Redondo Beach, California. ×10.6. (p. 595)
5—*Marcrurus anguliceps* Garman, from Station 2804 *Albatross* Expedition. ×14.6. (p. 579)
6—*?Coryphaenoides cinereus* Gilbert, from off Shumagia Island. ×12.5. (p. 579)
7—*Coelorhynchus argentatus* Smith & Radcliffe, from Station 5516, *Albatross* Expedition. ×23.6. (p. 579)
8—*Malacocephalus laevis* Lowe, from off Cape Colony, South Africa, ×30.2. (p. 579)

into small units by each row of spines, circuli slanting towards apical midaxis where they form a pointed angle. Ten to 11 rows of spines, 11 found in all larger scales; 10 spines in central row; numbers of spines in rows progressively decreasing laterally to 1 or 2 in the outermost rows. Spines rigid and strong set on protruding ridges on coarse side of scale: well marked grooves between spine ridges. Spines protruding beyond apical border never well preserved, seemingly varying in size. The scale is distinguished from the two most closely related forms, *P. zemorrianus* and *P. oregonensis*, by its shape with narrowing apical pole, degree of coarseness and exact spine count.

The scales of this species are more or less dominant in the lowermost portion of the Saucesian section in the Texas Newman well. They occur together with a number of other macrurid species, but are more abundant than any other species. Since rattails seem to be the only organisms represented in this section of the well, there can not be much doubt that it was laid down in very deep water, even though the section is very sandy in its major parts. An abyssal, or bathyal to abyssal, environment is indicated.

Comparison of Species

Scales of the three species of *Promacrurus* described above, *P. zemorrianus*, *P. oregonensis*, and *P. newmani*, represent a group of closely related species of that genus. Scales of this group evidently are very abundant in the lower Saucesian and more so throughout the Zemorrian section of California and the Pacific Northwest, representing a number of species which are sometimes difficult to distinguish. The same type of scale is also most commonly found among Recent rattails (*Macrurus anguliceps* and *Coryphaenoides cinereus*, Pl. 70, fig. 5–6 are examples). Minor differences in shape, number of spines, number of rows of spines, coarseness of circuli, and size differentiate the species from each other. Undoubtedly more species of this group will be found in the Pacific coast sections of that age.

Table 1 compares the characteristics of the three species described.

Promacrurus alseanus, n. sp.
Pl. 72, fig. 1; Text-fig. 13

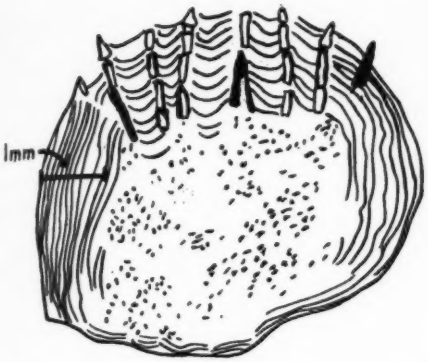
Holotype.—CIT 10483; 4.3 by 5.2 mm.

Type locality.—Yaquina formation, south side of Alsea Bay, in T. 13 S., R. 11 W., Willamette B. & M., Lincoln Co., Oregon.

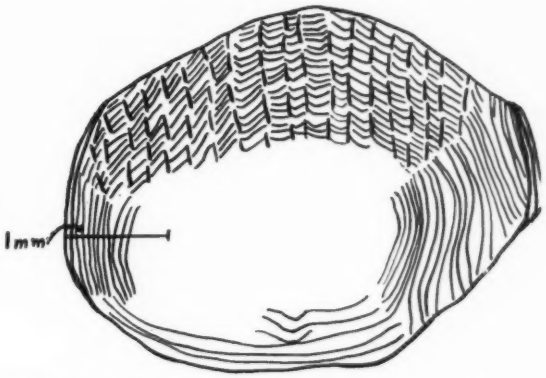
Description.—The specimen has the pattern of a regenerated scale, however this type of scale may be typical for this species which is characterized by great coarseness of its scales. Circuli restricted to external border of scale, more or less concentric with scale border, angulated in basal region; circuli coarse, 11 in 1 mm. distance. No nucleus apparent in type and only specimen; the large center of the scale ornamented by coarse markings and point shaped elevations. Eight rows of very coarse spines in apical area. Central rows best visible and clearly consisting of two

Table 1.—Comparison of Species of *Promacrurus*

	Ridges and spine rows	Circuli in 1 mm. ventrad from dorsal border	Size (mm.)	Shape	Number of spines in central row
			smallest greatest		
P. oregonenesis	9 to 10	16 to 20	length 2.2–3.67 by depth 3.2–4.67	1–1⅓	8
P. zemorrianus	13 to 16	20 to 28	length 3.0 –4.0 by depth 3.7 –4.33	1–1¼	10–13
P. newmanni	10 to 11	18 to 21	length 2.4 –4.3 by depth 2.67–5.40	1–1¼	10



TEXT-FIG. *13*—*Promacrurus alseanus*, n. sp. Holotype, from an outcrop on south side of Alsea Bay, Yaquina formation; 4.31 by 5.2 mm.



TEXT-FIG. *14*—*Promacrurus alferitziensis*, n. sp. Holotype, from the Standard Oil Co. well Alferitz No. 1, at 1366 to 1388 ft. depth; 3.4 by 4.7 mm.

spines each, which have been fractured in places.

The coarseness of the scale, as well as the eight subparallel rows of strong spines, distinguishes it from the others described here.

The scale was found together with the Zemorrian *Etringus* sp., *Paleobathygadus* sp., *Lampanyctus* sp., and other species of rattails. A bathyal to abyssal Zemorrian environment is clearly indicated.

The specimen shown (Pl. 72, fig. 2) is in the collection of the Richfield Oil Corporation, Long Beach. It was found at a locality not far removed from the one described above and may very well represent the same species because of its coarse appearance.

PROMACRURUS ALFERITZIENSIS, n. sp.
Text-fig. 14

Holotype.—CIT 10521; 3.4 by 4.7 mm.

Type locality.—Standard Oil Company well Alferitz No. 1, 250 ft. E., 200 ft. S., of center of Sec. 14, T. 25 S., R. 18 W., Mt. Diablo B. & M. Devils Den District, San Joaquin Valley California, at 1366–1388 ft. depth.

Description.—Coarse side of type and only specimen and its mold preserved. Scale comparatively large, pyritized, and quite coarse. Holotype possibly representing a regenerated scale, but in any case characterized by the great number of subparallel spine rows as a well distinct species. Circuli preserved in basodorsal and ventral portions of scale; these directed apicobasad, ending at basal border with an almost right angle, widely spaced, 16 in 1 mm. distance. Central scale portion almost smooth, possibly due to regeneration; three to four vague circuli surrounding basal border, indicating position of an original angulation close to midaxis of basal pole. A "microfault" around the central scale portion has caused deformation of basal pole due to irregular compression. No sign of a nucleus. Apical portion strong and well preserved. Circuli slanting from dorsal and ventral borders toward central midaxis, becoming more and more horizontal in center. Each row of spines interrupting circuli which change their direction slightly at these points of division. Twelve to 13 circuli in 1 mm. distance basad from apical border; intercircular spaces very wide. Nineteen rows of spines; central rows with 5 or 6 spines, numbers decreasing laterally as follows: 5,5,5,4,4,4,3,2,1 or 2. Rows in "non-regenerated" scales may have been longer, continuous to nucleus(?). Each spine touches the one placed distally to it; spines conical, pointed, none preserved beyond apical border.

The species is distinguished by its coarseness and great number and arrangement of spine rows. In the great number of subparallel spine rows it shows resemblance to *Amblygoniolepidus polystichus* (see below), but in the present species the number of rows is much larger, the intercircular apical spaces are wider and the scale is much coarser.

The scale was found in the Refugian section, San Lorenzo group, of the Standard Alferitz well, more particularly in the *Cibicides ungeriana* zone. The section is poor in fish forms, all recognizable fish remains belong to various species of rattails; most of these are not well enough preserved for description. The ecology during deposition must have been abyssal since a variety of rattails is present, while remains of shallower water fish forms are completely lacking.

PROMACRURUS ASYMMETRICUS, n. sp.,
Text-fig. 15

Holotype.—CIT 10522; 2.67 by 1.9 mm.

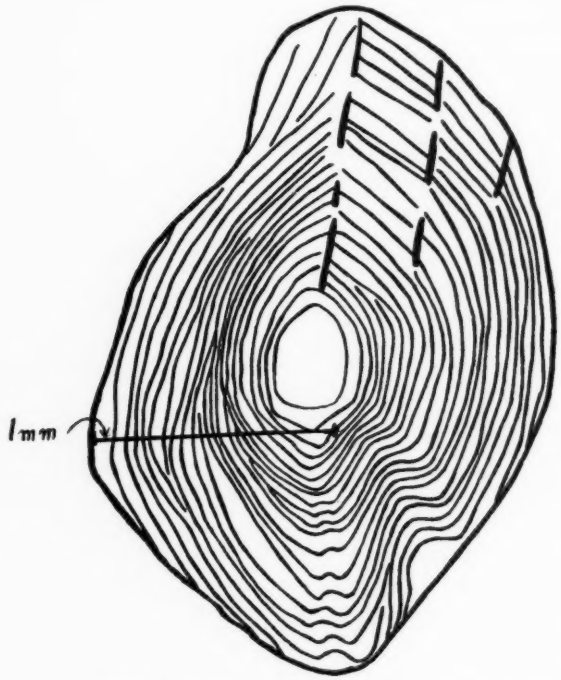
Type locality.—Standard Oil Co. well Alferitz No. 1, Sec. 14, T. 25 S., R. 18 W., Mt. Diablo B. & M., Devils Den district, San Joaquin Valley, California, at 1290–1291 ft. depth.

Paratype.—CIT 10523; 2 by 1.4 mm. from the same locality at 1273–1290 ft.

Description.—Coarse sides of type and paratype and mold of type preserved. Scales small, of exceptionally asymmetric shapes. Basal circuli moderately coarse, asymmetric, forming a fairly deep fold on ventral border, a distinct sharp angle near basal midaxis; circuli continuing dorsad from axis with a small fold, then with an indistinct wide angle in diagonal from nucleus to dorsobasal corner. About 21 circuli in 1 mm. distance extending from nucleus to dorsal border. Nucleus pear-shaped rather large. Intercircular spaces widening in apical region, not very distinct here. Ventral apical border widely convex, dorsal apical border deeply indented. End of apical extension obtuse. Three rows of spines, attached to ventral apical scale portion; spine numbers decreasing towards ventral border: 4, 3, 1. Spines forming deep rod shaped grooves where they were inserted, preserved by their molds only.

The scales are small, longer than deep, the apical pole widens on one side and shows a deep indentation at the other. Scales of this unusual shape were found at different horizons of the well; this seems an indication that they represent "a good species." No other macrurid scale is comparable to this species.

The scale occurs in strata of the Refugian, San Lorenzo group, in the *Cyclamina macra* zone of the Alferitz well. Scales are poorly preserved in this portion of the well; all those recognizable are rattails and the facies represents a deep-water environment, most likely of abyssal nature.



TEXT-FIG. *15*—*Promacrurus asymmetricus*, n. sp. Holotype, from the Standard Oil Co. well Alferitz no. 1, at 1290 to 1291 ft. depth; 2.67 by 1.9 mm.

PROMACRURUS SAUCESIANUS, n. sp.
Text-fig. 16

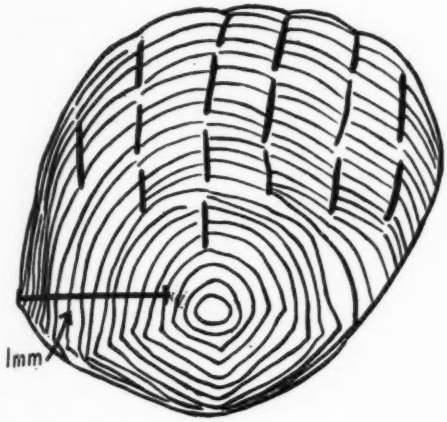
DAVID, 1944, Carnegie Inst. Washington, Pub. 551, no. 3, pl. 3, fig. 26.

Holotype.—CIT 10488; 2 by 2.67 mm.

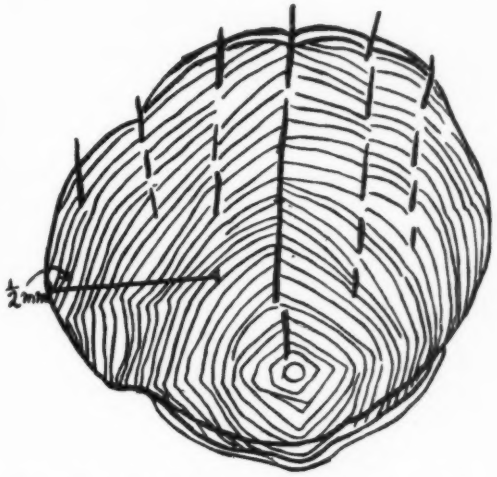
Type locality.—The Texas Co. well Newman No. 1, Sec. 23, T. 29 S., R. 28 E., San Bernardino B. & M., Kern River District, San Joaquin Valley, California, at 5423 ft. depth.

Paratypes.—CIT 10489–10490; from the same locality, same depth; 2 by 2 mm.; 1.67 by 1.67 mm. Basal portion of both specimens poorly preserved. CIT 10496, same locality, 5816–5848 ft. depth, 2.3 by 2.70 mm. probably belongs to the same species.

Description.—Scales small, comparatively



TEXT-FIG. *16*—*Promacrurus saucesianus*, n. sp. Holotype, from the Texas Co. well Newman no. 1, at 5423 ft. depth; 2+0.15 by 2.67 mm.



TEXT-FIG. *17*—*Promacrurus mimus*, n. sp. Holotype, from the Amerada Petroleum Co. well Beer no. 1 at 3540 ft. depth; 1.40+0.15 by 1.2 mm.

coarse; as deep as long or slightly deeper than long; scale narrowing towards apical border; dorsal and ventral borders slanting in direction of apical axis. Basal circuli forming definite pointed angles in basal midaxis and in diagonals from nucleus toward basodorsal and basoventral corners. About 18 circuli in 1 mm. distance dorsad from ventral border. Apical pole with six rows of spines, dividing apical region into seven stout coarse well distinct ridges; five spines in central rows, three in those dorsal and ventral to it, and two in outermost rows. Nucleus rounded approaching basal border somewhat more than apical end.

The scale is similar to *P. zemorrianus*, but is smaller and stouter, there are less apical ridges and spine rows. The shape differs in the narrow apical pole as compared to the basal region.

The scale is found in California Saucesian strata over a wide range. In the Texas Company Newman well it occurs in a deep-water environment where fragmented herring scales, shads and round herring occur together with a number of different rattail species.

PROMACRURUS MIMUS, n. sp.
Text-fig. 17

DAVID, 1944, Carnegie Inst. Washington, Pub. 551, no. 3, pl. 1, fig. 10.

Holotype.—CIT 10518; 1.40+0.15 by 1 mm.

Type locality.—Amerada Petroleum Co. well Beer No. 1, Sec. 17, T. 26 S., R. 19 E., Mt. Diablo B. & M., west of Williamson area at 3640 ft. depth, San Joaquin Valley, California.

Referred material.—CIT 10519–10520; 1.2 by 1 mm.; 1.33 by 1.2 mm., from the Standard Alferitz No. 1, Sec. 14, T. 25 S., R. 18 W. at 1290–1291 ft. depth.

Description.—A small species, almost round, but with somewhat truncate basal border. Basal circuli fine and closely approaching each other; 25 in 1 mm. distance in type; 22 in specimen from Alferitz well; 25 circuli ventral to nucleus and 16 dorsal to it in type; 20 and 12 respectively in specimen from Alferitz well. Angles in basal midaxis obtuse and flattened by truncate basal border, angles in diagonals from nucleus to basodorsal and ventral corners obtuse and indistinct, dislocated toward basal border. Circuli continuing into apical portion of scale where intercircular spaces widen considerably. In type, 25 circuli apicad of nucleus, 20 in specimen from Alferitz well. Circuli slanting towards central apical axis, but only slightly so; circuli not as markedly interrupted by rows of spines as in some of the larger species.

Small, rounded shape, delicate structure, and truncate basal pole distinguish this species.

The species occurs in San Joaquin Valley localities of Oligocene (Refugian) age. In

the Alferitz well the species occurs in strata where only rattails were found indicating deep water of abyssal nature. In the Amerada Beer No. 1 a mixed assemblage of fish remains was found in the strata with this species (see David, 1944, pp. 29–30). This assemblage, so far only known from this location is not well known. The specimen illustrated by David (1944, pl. 1, fig. 7) belongs, however, to the family Albulidae rather than to the Halosauridae, as suggested. *Albula*-like scales were found in similar assemblages in the Texas Careagra well and the Nye mudstone of Yaquina Bay, Oregon, and seem likely to be represented by one or very few specimens in deep-water deposits. Of the five forms found in the assemblage, two indicate deep-water, the "iniomi" and the rattail. The albulid is a neritic pelagic form; the remaining two forms are undetermined. It does not seem justifiable to give a definite ecological determination of this location at this time.

PYKNOLEPIDUS, n. gen.

Type species.—Pyknolepidus macrospinosus n. sp.

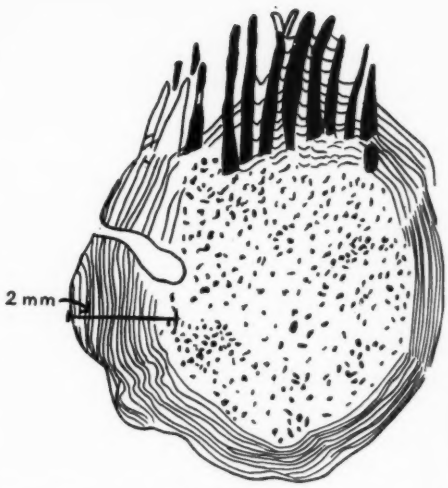
The genus is distinguished by the huge spines inserted in a fairly close-set group in the central portion of the apical border. The scale is the coarsest anacanthid form found so far in the entire region. It comes closest to *Promacrurus alseanus*, but is markedly distinct in its apical pattern.

PYKNOLEPIDUS MACROSPINOSUS, n. sp.
Text-fig. 18

Holotype.—CIT 10482; 8.3 by 7 mm. The length includes the spines.

Type locality.—Yaquina formation, on south side of Alsea Bay, in T. 13 S., R. 11 W., Willamette B. & M., Lincoln Co., Oregon.

Description.—The very large coarse type may represent a regenerated scale since no nucleus is indicated and the large center of the scale is marked by coarse pustulations and point-shaped markings. Irregular, concentric circuli surround outer borders of scale; these interrupted in places most likely due to pressure during preservation. Circuli forming irregular angulations in basolateral angles and midbasal axis. Apical



TEXT-FIG. *18—Pyknolepidus macrospinosus*, n. sp. Holotype, from outcrop south side of Alsea Bay, Yaquina formation, Oregon; 8.3 by 7 mm.

circuli coarser than basal ones, 20 circuli in 1 mm. distance in basal region, 10 in apical area of scale. About eight or nine robust parallel spines set close together on apical rim. Each spine may have represented an entirety originally; in the present state of preservation irregular division lines are visible that obviously represent breakage points, caused by pressure during the preservation process. The longest spine measures 2.33 mm. in length.

The scale is not comparable to that of any other known species.

At the type locality the species was found to occur with the Zemorrian *Etringus* sp., *Paleobathygadus* sp., *Lampanyctus* sp., and a number of other rattail species. An environment of Zemorrian bathyal to abyssal character is clearly indicated.

HOMEONEZUMIA, n. gen.

Type species.—Homeonezumia multispinosus, n. sp.

The scales are longer than deep. The rounded basal circuli form wide obtuse angles in mid and laterobasal diagonals. The apical region is covered with a multitude of flattened spines, overlapping each other. The general appearance of the scale is similar to the Recent genus *Nezumia*, but the apical pattern clearly distinguishes it.

HOMEONEZUMIA MULTISPINOSUS, n. sp.
Text-fig. 19

DAVID, 1944, Carnegie Inst. Washington, Pub. 551, no. 3, pl. 2, fig. 17.

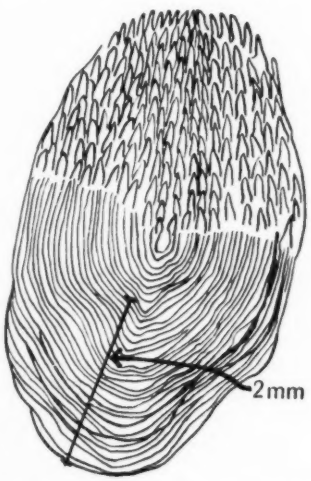
Holotype.—CIT 10503; 5 by 3.33 mm.

Type locality.—Texas Co. well Pioneer Unit Plan No. 1, Sec. 33, T. 11 N., R. 23 W., San Bernardino B. & M., Southern Sunset district, San Joaquin Valley, California, at 5459–5462 ft. depth.

Paratype.—CIT 10504; 5 by 3.67 mm., from the same well at 6478 ft. depth.

Description.—Scale much longer than deep. Elongate basal portion with rounded circuli forming fairly distinct pointed angles in basal midaxis; and obtuse angles in diagonals from nucleus to dorso- and ventrobasal corners. Basal circuli approaching each other closely, 19 to 20 in 1 mm. distance ventrad from dorsal border. Nucleus rounded, central. Apical pole densely covered by overlapping spines, inserted in imbricated fashion. Spines flattened, double edged, with fairly stout bases; spines longer than wide, about 0.35 mm. long; set too closely together to be counted accurately. Scale was probably fairly adherent to body, since a piece of skin was found at same locality with a number of scales attached.

Shape and spine pattern distinguish this species from all other macrurid scales.



TEXT-FIG. *19*—*Homeonezumia multispinosus*, n. sp. Holotype, from the Texas Co. well Pioneer Unit Plan No. 1, at 5459 to 5462 ft. depth; 5 by 3.33 mm.

The species occurs in strata of the Pioneer Unit Plan well where various species of rattails abound; the halosaurid *Laytonia californicus* David is not rare. An abyssal Zemorrian environment is clearly indicated.

AMBLYGONIOLEPIDUS, n. gen.

Type species.—*Amblygoniolepidus polystichus*, n. sp.

The genus is distinguished by scales that are much deeper than long with widely rounded basal circuli and a great number of subparallel rows of small spines in the apical region. The only other genus that shows such a large number of spine rows is *Promacrurus alferitziensis;* but the scales of the latter are much coarser and the spines more robust.

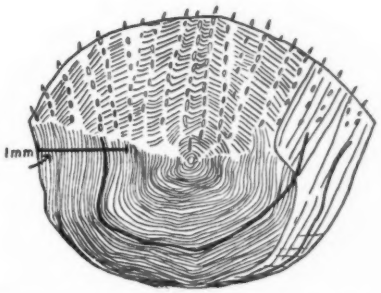
AMBLYGONIOLEPIDUS POLYSTICHUS, n. sp.
Text-fig. 20

DAVID, 1944, Carnegie Inst. Washington, Pub. 551, no. 3, pl. 2, fig. 19.

Holotype.—CIT 10502; 3+0.30 by 4 mm.

Type locality.—Texas Co. well Pioneer United Plan No. 1, Sec. 33, T. 11 N., R. 23 W., San Bernardino B. & M., Southern Sunset district, San Joaquin Valley, California, at 5688 ft. depth.

Description.—Only one scale of the species included in the CIT collections, even though the species is probably more abundant at the locality. Basal pole very wide; basal circuli forming wide half circles, very obtusely angled in basal midaxis and laterobasal diagonals. Lateral angles slightly asymmetrical, not exactly coinciding with the diagonals from nucleus to basodorsal



TEXT-FIG. *20*—*Amblygoniolepidus polystichus*, n. sp. Holotype, from the Texas Co. well Pioneer Unit Plan No. 1, at 5688 ft. depth; 3+0.30 by 4 mm.

and ventral corners. Keel-like ridges extending from nucleus to these corners. Basal circuli fine, set close together, 32 in 1 mm. distance ventrad from dorsal border. Nucleus rounded to pear shaped, its distance from apical border one third time that from basal border. Apical pole well distinguished, apical circuli becoming coarser, slanting towards central axis at both sides and interrupted by each row of spines. Nineteen rows of spines; eight spines in central row, lateral rows decreasing in numbers progressively, as follows: (8),7,6,5,4,4,3,2,2, 1. Hardly any of the spines distinctly discernible, only short rod-like impressions clearly marked on body of scale. Some of spines protrude beyond apical border preserved, pointed and about 0.30 mm. long.

The scale is easily distinguished from all others by its great depth as compared to length and by the great number of rows of small spines.

The species occurs in the middle Zemorrian (*Siphogenerina nodifera* zone) of the Pioneer Unit Plan well, a range of the well that was deposited in an abyssal environment, as indicated by its abundance of rattails, occasional presence of Halosauridae, and the absence of other well preserved fish forms.

OXYGONIOLEPIDUS, n. gen.

Type species.—*Oxygoniolepidus washingtonensis*, n. sp.

The genus is distinguished from all others by scales that unite the following characteristics: they are longer than deep and hexagonal in shape; the scale outlines show sharp angles in basal and apical regions; a comparatively large number of long parallel rows of spines ornaments the apical area. The only other genus with scale of similar shape, *Homonezumia*, is more rounded and has wide, overlapping, flattened spines.

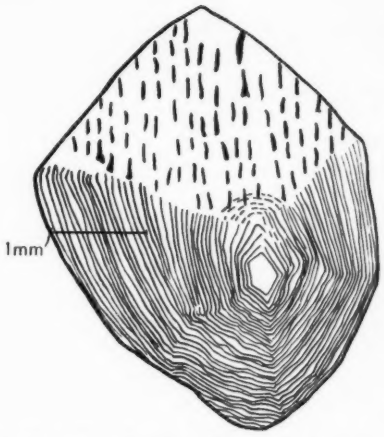
OXYGONIOLEPIDUS WASHINGTONENSIS, n. sp.

Text-fig. 21

Holotype.—CIT 10524; 5.4 by 3.5 mm.

Type locality.—An outcrop near the town of Arctic in western Washington, latitude 123° 43′, west longitude 46° 52′ 50″, north Willamette B. & M.

Description.—Species presented by a single specimen. Scale longer than deep and



TEXT-FIG. *21—Oxygoniolepidus washingtonensis*, n. sp. Holotype, from an outcrop near Arctic in Western Washington; 5.4 by 3.5 mm.

irregularly hexagonal. Irregularity and slight asymmetry probably caused by pressure during preservation. Basal portion of scale elongate, the numerous basal circuli forming a distinct pointed angle in basal midaxis, and obtuse angles in diagonals from nucleus to basolateral corners; circuli wavery, not always parallel and forming small irregular folds. Nucleus forming a somewhat distorted octagon. About 27 basal circuli dorsal to nucleus, 40 ventral to it; about 23 in 1 mm. distance dorsad from ventral border. Extreme rim of dorsal basal sector of scale may not be preserved and this could explain the difference in numbers of dorsal and ventral circuli. Fine circuli extending into apical pole; these not very distinctly preserved (not shown in Text-fig. 21). Intercircular spaces not widening in apical region. Numerous spines covering apical region; some of these given the appearance of a split in their basal portion into small double roots, others are only partly preserved. These spines seem to continue in the matrix to the opposite scale surface. Number of spine rows, 19; number of spines in rows dorsal to ventral approximately: 1,2,3,4,5,5+1?,6,4(+2 missing?), 6,4(+2 missing?),6+1,7,7?,5,5,4,4,3,2,2,1. Few spines, if any, are preserved protruding apical border.

The scale is easily distinguished from all other macrurid forms by its 19 long rows of spines and the hexagonal shape.

The assemblage in the outcrop section

includes the Zemorrian round herring, an undescribed genus of herring, *Paleobathygadus yaquinensis*, *Lampanyctus* sp., *Laytonia californicus*, *Promacrurus oregonensis*, and other rattails. A deep-water environment of bathyal to abyssal character is indicated.

HOMEOCORYPHAENOIDES, n. gen.

Type species.—*Homeocoryphaenoides chiasmacanthus*, n. sp.

The scales of this genus are of moderate size, a little deeper than long. Long spinules are attached in diffuse arrangment to the apical pole. The scale shows similarities to scales of the Recent species *Coryphaenoides rupestris* Gunnerus (Parr, 1946, fig. 24, no. 13), but the fossil form has finer circuli, is of more rounded shape, and has much longer spines.

HOMEOCORYPHAENOIDES CHIASMACANTHUS, n. sp.
Text-fig. 22

DAVID, 1944, Carnegie Inst. Washington, Pub. 551, no. 3, pl. 3, fig. 27.

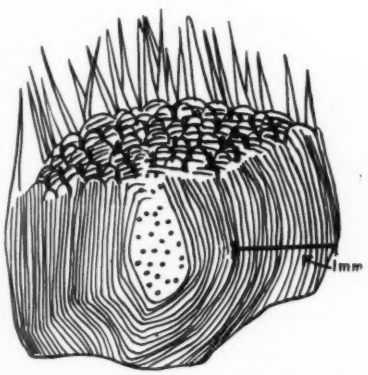
Holotype.—CIT 10491; 2.67+0.8 by 3.33 mm.

Type locality.—Texas Co. well Newman No. 1, Sec. 23, T. 29 S., R. 28 E., San Bernardino B. & M., Kern River District, California, at 5741 ft. depth.

Description.—Only one specimen of this pretty little scale is known. Coarse side embedded in matrix, smooth side showing. External basal circuli penetrating toward smooth side and discernable as very fine and close set lines; about 25 in 1 mm. distance dorsad from ventral border. Midbasal angle of basal circuli pointed, obtuse and asymmetrical, approaching dorsal scale border more than ventral one. Angles in diagonals from nucleus to basolateral corners obtuse, continuing basally in wavery irregular lines. Nucleus not recognizable. Apical pole well distinguished, apical circuli coarser than basal ones, rounded, interrupted by distinctly marked spine attachments; these are arrayed in an imbricate fashion. There may be about 14 or 15 rows of spines. Spine attachments in nuclear area not discernible and exact number of spines in each row can not be counted. Some 20 or more long slender pointed spines preserved extending beyond apical border; these originating from points of varying distance basad to apical border; all spines of similar length, about 0.80 to 0.85 mm. Central spines attached at apex of the rounded apical border extending farthest beyond border; spine tips as a whole forming a circle parallel to round rim of apical pole border.

The long slender spines, irregularly crossing each other in the apex of the apical pole easily distinguish this species from all other macrurid scales; the circuli are fine and the scale as a whole is delicate.

The scale originates from the lower portion of the Saucesian section of the Newman well, where rattails abound; hardly any other well preserved scales are present. The deposit must have been laid down in deep water most likely of abyssal nature. Sandy strata are prevalent throughout the section where the rattails occur.



TEXT-FIG. 22—*Homeocoryphaenoides chiasmacanthus*, n. sp. Holotype, from the Texas Co. well Newman No. 1, at 5741 ft. depth; 2.67 +0.8 by 3.33 mm.

CALILEPIDUS, n. gen.

Type species.—*Calilepidus lauxei* n. sp.

The very large scale of the genus is outstanding. It is much longer than deep, the apical portion takes up about one third of the scale length only. The basal portion of the type is asymmetric, midbasal and basolateral angles are sharp and distinct. The apical pole is beset with numerous spines of moderate length; they are strong, arranged in quincunx fashion and not in horizontal rows. The scale may show similarities to the Recent genus *Caribrurus*, but it differs in its proportions and in the great number of apical spines.

CALILEPIDUS TAUXEI,* n. sp.
Pl. 72, fig. 5

Holotype.—CIT 10501; 6.2+0.40 by 4 mm.

Type locality.—Texas Co. well Newman No. 1, Sec. 23, T. 29 S., R. 28 E., Kern River District, San Joaquin Valley, California, at 5800 ft. depth.

Referred material.—CIT 10516 from ca. 3000 ft. south of Mist, Keasey Quadrangle, Oregon.

Description.—Only one specimen of this large, rather beautiful scale was found. Smooth side of scale and mold of same side preserved. Circuli penetrating to and visible from smooth scale surface of the probably delicate scale. Scale much longer than deep. (A small triangle from basal portion of scale broken off.) Basal circuli with sharply pointed angles in midbasal axis; axis asymmetrical approaching dorsal side of scale. Circuli in diagonals from nucleus to basolateral corners irregularly folded and wavery; a distinct fold formed at basodorsal corner where scale is slightly indented. About 23 circuli in 1 mm. distance diagonally ventrad from dorsal border. Nucleus visible from preserved side of scale, twice as much removed from basal than from apical apex. Apical pole well differentiated due to ornate arrangement of the innumerable spines. These attached close to each other in imbricated fashion; spine rows seemingly forming diagonals ending at midaxis of apical pole, or crossing it at their midpoint and extending to apical border at opposite side of axis. About 28 rows of spines. Spines not completely visible since attached to coarse scale surface and pointing downward into matrix. Spine attachments and roadshaped spine bodies discernible, probably corresponding to only part of spine length. Spines directed toward center of scale. Spines protruding beyond apical border well preserved and complete; 19 to 20 in number; 0.40 mm. long. Spines not overly stout, narrowing toward their pointed ends.

A scale fragment from the Keasey formation is doubtfully referred to this species. Not much more than the apical portion of the scale is preserved, measuring 4.33 by 4.67 mm. The scale portion is well preserved and shows close similarity to *C. tauxei*. The apical pole length in both specimens is 3.67 mm. The arrangement of the spines and their preservation seems identical. There are 22 to 23 rows of spines in the Keasey specimen, 12 spines in the central row. About 21 circuli are in 1 mm. distance ventrad from the dorsal border. Few spines are protruding beyond the apical border, those that are have the same shape and about the same length as found in *C. tauxei*. Both specimens are nearly related. The size and shape of the scale (considering the apical portion only in the fragment) and the spine arrangement easily distinguish this form from all others.

The type is of Saucesian age and comes from the lower part of that section. The Keasey specimen is of Refugian age. Ecology in both localities is very similar. In both locations rattails are very abundant, and they represent undoubtedly deep-water assemblages while at the same time both sections are very sandy. If both specimens represent the same species it would have a comparably long range of existence.

LEPTACANTHOLEPIDUS, n. gen.

Type species.—*Leptacantholepidus delmontianus*, n. sp.

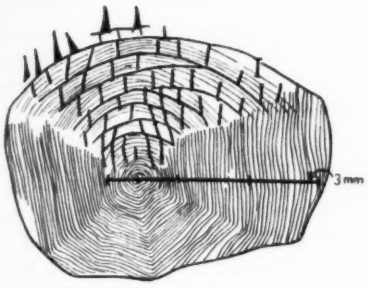
The scales are delicate and have a flexible appearance. Elongate, thin, rodlike spines are arranged in rows, but are seemingly only loosely attached to the scale body and easily displaced from their original position. The scales of this upper Miocene genus are not as coarse as most of the Saucesian-Zemorrian species. No other fossil or living genus seems comparable to this form.

LEPTACANTHOLEPIDUS DELMONTIANUS, n. sp.
Pl. 72, fig. 4; Text-fig. 23,24

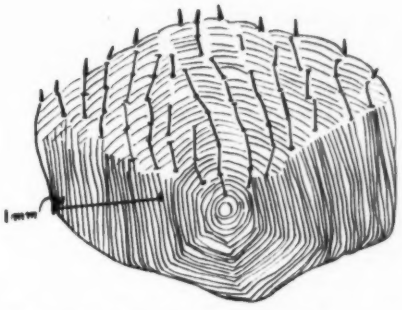
Holotype.—CIT 10487; 3.67+0.25 by 4.67 mm.

Type locality.—Ohio Oil Co. well Bear State No. 23, 1005 ft. N. & 944 ft. W. of L/C Sec. 30, T. 28 S., R. 21 E., Mt. Diablo B. & M., Elevation 676 ft., Belridge Oil Field, Kern Co., San Joaquin Valley, California at 4434 ft. depth.

* This species was named for Dr. Newlon Tauxe, who very kindly helped in finding appropriate names for many of the new species and genera described in this paper.



TEXT-FIG. *23*—*Leptacantholepidus delmontianus*, n. sp. Holotype, from the Ohio Oil Co. well Bear State No. 23, at 4434 ft. depth; 3.67 +0.25 by 4.67 mm.



TEXT-FIG. *24*—*Leptacantholepidus delmontianus*, n. sp. CIT 10484 from the General Petroleum Oil Co. well Mocco No. 218 at 1775 ft. depth; 2.67+0.14 by 3.33 mm.

Referred material.—CIT 10484–10486; 2.67+0.2 by 3.33 mm.; 2+0.2 by 3 mm.; and a fragmented specimen; all three come from the General Petroleum Oil Co. well Mocco No. 218, Sunset District, 2237 ft. north and 2192 ft. east of SW corner of Sec. 35, T. 12 N., R. 24 W., at 1775 ft. depth.

Description.—Scales oblong. Basal circuli close set. Midbasal sector seemingly weak in all scales and easily damaged; dorsal and ventral portions of scale more resistant. Basal circuli in type most distinctly angled in diagonal from nucleus to dorsobasal corner; angles in midbasal axis and in diagonal from nucleus to basoventral corner much more rounded (Pl. 72, fig. 4, drawings, Text-fig. 23,24, show diagrammatically restored scales in this respect). Circuli rather fine in basal section; 24 in 1 mm. distance ventrad from basodorsal border of type; 23 in same distance of specimen 10484; about 26 to 31 diagonally towards nucleus apicad from basal border of type. Nucleus closer to basal border, at a distance of two-fifths length of scale apicad from basal border. Nucleus surrounded by 4 to 6 fine rounded circuli. More external circuli increasingly angular. Circuli in midbasal sector showing an irregular wavery appearance. Apical pole rounded, distinctly differentiated from basal section of scale. The apical circuli rounded toward central axis, distinctly divided by spine rows into small curved sections. Scales obviously delicate, apical pole of type concentrically folded by compression of matrix. Spines delicate, seemingly dislodged from original position. Pattern of unsevered scale best shown by CIT 10484 (Text-fig. 24). Nineteen rows probably existed in type, 9 each side of central row; in CIT 10484 15 rows can be distinguished. Rows of spines curved, slanting toward central apex; number of spines decreasing progressively towards dorsal and ventral extremities, outermost rows with one spine only. (In the type the spines seem to have an imbricated arrangement in places where the scale is most strongly compressed into folds by the compaction of the matrix, this is probably not the original pattern.) Spines on body of scale forming slender rods, truncate at both ends, either loosely attached to next distal spine or dislodged by a small distance from successive spine. Spines protruding beyond apical border much more robust, conical with sharply pointed ends.

The following characteristics distinguish the species from the scales of all other known forms: the scales are deeper than long, of delicate structure, the apical pole is rounded; most characteristic are the elongate rod-like, easily dislodgeable spines. There are minor differences between type and referred materials, in size of apical border spines, in length of scales; the difference in spine pattern is thought to be caused by preservation.

The type comes from the *Bolivina brevior* zone, in upper Mohnian McLure shale; the other specimens are probably of Delmontian age. In both localities the scales occur in a deep neritic environment, accompanied by a varied well represented neritic assemblage consisting of scad mackerels, yellowtails, *Thyrsocles*, *Lompoquia*, shads, round herrings, herrings, etc. *Leptacantholepidus* is

not uncommon. The sediments were most likely assembled in a deep portion of the sea very close to the bottom of a neritic habitat.

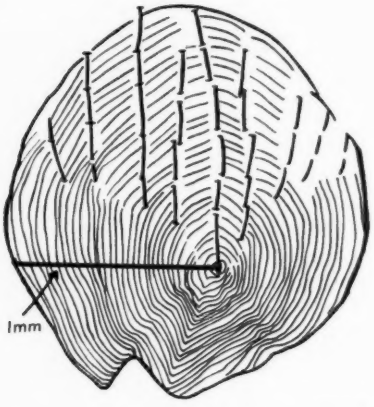
LEPTACANTHOLEPIDUS ROTUNDUS, n. sp.
Text-fig. 25

Holotype.—CIT 10492; 2 by 1.67 mm.

Type locality.—Ohio Oil Co. well Bear State No. 23, Sec. 30, T. 28 S., R. 21 E., Mt. Diablo B. & M., elevation 676 ft., in Belridge Oil Field, Kern Co., San Joaquin Valley, California, at 4212 ft. depth.

Paratypes.—CIT 10493–10495; 2.33+0.33 by 2 mm.; 1.67 by 1.67 mm.; and 1.33+0.33 by 2 mm., from the same well.

Description.—Scales delicate, small, round. Type and two other specimens very slightly longer than deep, one scale a little deeper than long. All four specimens well preserved. Nucleus rounded approaching basal border, about one-third of scale length apicad of basal border. Type with a triangular indentment at one side of basal mid-axis. All other specimens symmetrical. Angles of basal circuli pointed in basal mid-axis, more obtuse in diagonals from nucleus to laterobasal corners. Basal circuli fine, about 31 in 1 mm. distance ventrad of dorsal border. Apical pole rounded, not very clearly differentiated from basal portion of scale. Rows of spines very clearly marked. Spines slender, rodlike; spines loosely attached to each other, sometimes slightly dislodged and small spaces left between consecutive spines. Central row with five or six spines, usually four rows of spines dorsal and ventral to it, spines in each row decreasing in numbers towards dorsal and ventral extremities as follows: 5, 5 or 4, 3, 2. Spine rows distinctly curved and directed towards center of apical scale border. Length of spines about 0.30 to 0.35, spines comparatively long considering size of scales.



TEXT-FIG. *25—Leptacantholepidus rotundus*, n. sp. Holotype, from the Ohio Oil Co. well Bear State No. 23, at 4212 ft. depth; 2 by 1.67 mm.

The species is well distinguished by its small rounded shape, a central row of spines dividing two groups of slanting rows of spines, and by its slender, rodlike loosely attached spines.

The species occurs in the *Bolivina brevior* zone of the upper Mohnian McLure shale. A deep neritic environment is indicated, most likely in a deep basin beyond the neritic zone whereto the well represented and well preserved neritic fish remains were transported by currents for a short distance down the slope. Rattails as well as the accompanying scales of neritic fishes are well preserved.

HOMEOMACRURUS, n. gen.

Type species.—Homeomacrurus fernandensis, n. sp.

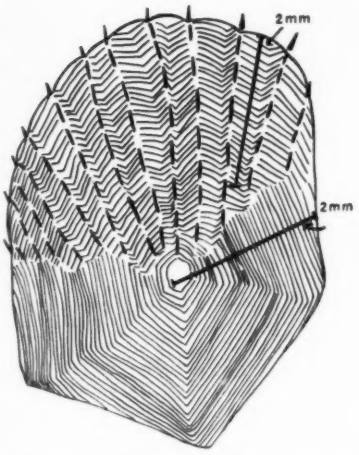
Scales much longer than deep, basal pole with sharply pointed angles, apical pole with rounded border; the rather coarse scales come close to the basic pattern of the macrurid scale. The course of the circuli is very regular, they form definite distinctly pointed angles in the midbasal and laterobasal diagonals. Intercircular spaces are rather wide. The nucleus is hexagonal. Like the scales of the genus *Promacrurus* the scale pattern is similar to the basic macrurid pattern, but the scale shape differs; the scales are much longer than deep; they are larger, coarser and have wider intercircular spaces.

HOMEOMACRURUS FERNANDENSIS, n. sp.
Pl. 72, fig. 3; text-fig. 26

Holotype.—CIT 10505; 4.5+ (the basal portion missing) by 4.5 mm.

Type locality.—The Texas Co. well Towle No. 1, Hasley Canyon, Castaic area Sec. 4, T. 4 N., R. 17 W., San Bernardino B. & M., at 4772 to 4781 ft. depth.

Paratypes.—Two specimens, 4.7 by 4 mm. and 3 by 3.6 mm. Both specimens incomplete with the basal portion and in the latter



TEXT-FIG. 26—*Homeomacrurus fernandensis*, n. sp. Drawn diagrammatically from specimens coming from the Texas Co. wells Towle No. 1 and Fernando No. 1 of upper Delmontian to lower Pliocene Pico formation strata. About 5.5 to 4.5 mm.

also the central portion of the apical pole missing; both come from the same well at 4565 to 4575 ft. depth.

Referred material.—Five specimens, the more complete ones measuring 5 by 3.6 mm.; 4.4 by 3.5 mm.; a portion of the basal pole is always missing and three specimens show only part of the apical pole preserved. The specimens come from the Texas Co. well Fernando No. 1, Sec. 11, T. 4 N., R. 17 W., San Bernardino B. & M., at 5510 to 5520 ft. depth, 5555–5565 ft., 5575–5578 ft., 5584–5589 ft., and 5615–5625 ft. depth respectively.

Description.—Scales rather large, longer than deep. (Considering the apical pole structure and the position of the nucleus, in their relation to the basolateral corners, which are most often preserved, it is possible to reconstruct the basal pole where missing.) Basal circuli fine and close together, about 30 in 1 mm. distance dorsad from the ventral border of type. About 42 circuli altogether ventrad of nucleus. Nucleus small and hexagonal. Circuli in apical pole becoming much coarser than in basal and central portions, distinctly divided into sections by rows of spines. Each individual section of apical circuli distinctly arched in grooves between adjacent spine rows. About 16 to 17 circuli in 1 mm. distance basad from apical border. Type with 13 rows of spines, 10 to 11 in other specimens or a few more not distinctly preserved. Spines forming fine rods, none of them very long, 7 to 9 are judged to be in the central row.

The species is interesting because it occurs rather abundantly in the Pliocene (lower Pliocene Pico formation in Texas Fernando well) or uppermost Delmontian (Texas Towle well) strata; few other fish forms are known from this age in California. The species is distinguished by its large size, the scale is longer than deep; has fine circuli for its size in the basal region, coarse circuli in the apical pole region; there are at least 13 rows of spines in large specimens, and almost certainly more than seven spines in the central row. These characteristics distinguish the species quite clearly in spite of its poor preservation. The abundance of the species is remarkable.

Laytonia was described from the same sections of these wells (David, 1948). The abundance of the macrurids and the presence of this deep-water Heteromi indicate that these sections were laid down in very deep water, in or close to an abyssal environment.

Remarks.—In the two localities where this species was found, it occurs in a sandy, micaceous matrix that does not split evenly. The preservation of the material therefore is very poor, none of the specimens are complete, especially the basal portion is usually missing; the sandy porous condition of the matrix does not allow very precise outlines of detail structures. However because of the abundance of the species in these localities it was possible to reconstruct the pattern of the scale diagrammatically. (More specimens than those preserved were found in the original material; also this material when freshly split shows more details.)

Family MERLUCCIIDAE
Pl. 70. fig. 4

Scales from specimens of *Merluccius productus* (Ayres) from Southern California were studied. The largest scale measured 7.3 by 5 mm. Peabody (1931, p. 150) describes a scale of *M. bilinearis* (Mitchell). Belloc (1929, p. 237) described scales of *M. merluccius* (Linnaeus) of different ages,

shown in his fig. 32,33,37,38. The scales of *Merluccius* are oval; the nucleus is more or less central; it forms a very small ovoid with pointed angles in the midaxis apically and basally. The nucleus is surrounded by fairly concentric circuli (in the photo, Pl. 70, fig. 4, the nuclear region is not clearly visible due to overlying skin). Concentric circuli continue in regular succession throughout most of the scale; only the dorsalmost and ventralmost circuli may end at the basal and apical borders without completing a full circle of the scale's periphery. Definite pointed angles are formed in the midaxis of apical and basal portion. These angles are sharper in the apical region where the circuli approach each other more closely. In the basal region of attachment the intercircular spaces widen more and more toward the border, the angles may become irregular, two or more angulations may form in the most peripheral apical region. An irregular pattern of cross bars divides the intercircular spaces of the basal region. This pattern is not clearly marked over the entire region and does not seem to extend equally over the apical pole but is more outstanding in certain sections. The crossbars extend from one circulus to the next in irregular directions, dividing the intercircular spaces into many irregularly shaped cubicles. This pattern is not comparable to the very conspicuous coarse pattern known from the genus *Gadus*. It also differs visibly from the pattern described for *Bregmaceros* and *Bathygadus*, and the Phycinae (see above).

In *M. bilinearis* as described by Peabody this pattern seems to be more strongly marked than in *M. productus*. Otherwise the scale characteristics of the various species do not show much difference, except for detail variances in proportions. The fully concentric circuli showing parallel pointed angles in the midaxis of basal and apical regions easily distinguish the scales of this genus from any of the known gadid scales.

Ecologically the genus *Merluccius* has an interesting distribution (Hart, 1948). The genus inhabits warm temperate and subtropical seas. Hakes undertake seasonal migrations and are found in comparatively shallow water in the summer; they proceed far off shore in the winter, farther than most of the fishes that undertake similar migrations. In winter their range extends beyond the edge of the continental shelf over oceanic depths. It is particularly interesting that Barnard (1925) states that Macruridae are prominent in the diet of the South African species of *Merluccius*. The seasonal migration of *Merluccius* is known for the European *M. merluccius* (Linnaeus), *M. australis* (Hutton) and for *M. bilinearis* (Mitchell). The latter species is said to occur in Tortugas, Florida, also (Longley & Hildebrand, 1941), but here "this common northern fish of both shallow and deep water occurs only in deep water, of 140 to 392 fathoms."

PROMERLUCCIUS David, n. gen.

Type species.—Promerluccius venturaensis, n. sp.

The scales of this genus may be distinguished from the Recent genus by the more irregular course of the peripheral apical circuli. These do not form a definite pointed angle in the apical axis but form one to several folds. The nucleus approaches the basal border more closely than the apical rim. Scales are small to medium sized.

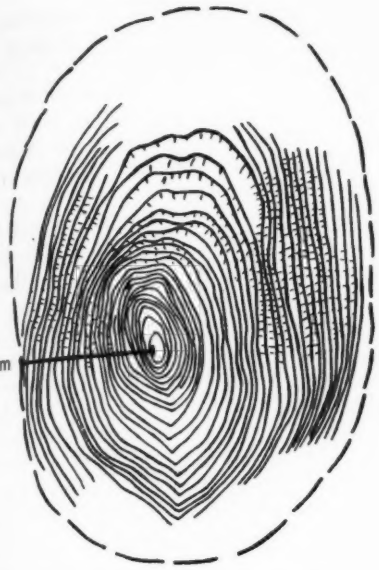
PROMERLUCCIUS VENTURAENSIS, n. sp.
Text-fig. 27

Holotype.—CIT 10517; 3.4 by 2.6 mm.

Type locality.—Oxnard Oil Co. well Vanoni No. 1, Sec. 10, T. 1 N., R. 21 W., San Bernardino B. & M., Ventura Co., at 5023–5048 ft. depth.

Paratypes.—Other specimens found in the same well and in wells nearby are preserved in the Richfield Oil Corporation Paleontological Laboratory in Long Beach.

Description.—The scale is well preserved, put possibly not quite complete in its periphery. Nucleus very small, forming a small ovoid, pointed toward the basal pole and rounded at its apical side. Nucleus probably approached basal border in complete scale, distance nucleus to apical border about one-fifth that of nucleus to basal border in complete scale. Nucleus surrounded by concentric circuli; in basal region these form one definite pointed angle each in midaxis or close to it; 18 to 20 circuli can be counted. In apical region the centralmost circuli rounded with an indefinite indication of angulation in midaxis, intercircular spaces widening more and more toward periphery; in the peripheral apical region the circuli become saddle-shaped,



TEXT-FIG. 27—*Promerluccius venturaensis*, n. sp. Holotype, from the Oxnard Oil Co., Vanoni No. 1, at 5023 to 48 ft. depth; 3.4 by 2.6 mm.

and form two to three microfolds; 20 to 22 circuli can be counted. The circuli are not perfectly concentric. The innermost region seems to have been pressed out of place by preservation conditions; this gives the scale a slightly distorted appearance. Ventral and dorsal circuli parallel in apico-basad direction, ending in basal and apical borders without completing a full circle around the scale.

The scales of the species are distinguished most definitely by the pattern of the apical region where the circuli are irregularly folded.

The scales of this species occur together with *Progadus pliocenicus* David, undetermined fish bones, vertebrae, and a few other uncertain forms in the Pliocene of the Ventura Basin. This combination of forms may indicate a bottom fauna in fairly deep water, neritic to slightly deeper. Temperature of the water would effect depth of occurrence of these forms.

ANALYSIS OF PISCINE ASSEMBLAGES

Species, Faunal Assemblages and Ecology

The series of species described in this report show that an unexpectedly large number of anacanthin forms are preserved in the Oligocene-Miocene-Pliocene strata of the North American Pacific coast section. Altogether 32 species are listed, coming from 22 localities. Others were found but were not sufficiently preserved or otherwise distinctive enough for description.

Most of the species are known from their scales only, the scales show characteristics so distinctive that multiple description of the same species from different scales need not be feared. Five species, four of the genus *Eclipes*, and one of *Bolbocara*, have been described from skeletal remains. While the scales of these forms are not known, it is possible that they are represented also by some of the scales described.

Table 2 lists all extinct anacanthin species considered in this paper, together with the total number of piscine species that accompany each species at the type localities. This table shows that the total number of species represented by each scale assemblage is rather small (average of seven to eight species). A large amount of material was investigated for each locality, a sufficient amount to ascertain that all regularly occurring members for each assemblage were found. From outcrop sections several large samples, some of these carefully chosen for the abundance of fish remains, were chipped and examined for scales. In other cases each sample of a continuous section of closely spaced samples was examined. Assemblages from cores are usually represented in oil well core sections of considerable depth, and portions of each core were examined.

In outcrop sections where fishes were preserved as complete skeletons, anacanthin forms occurred in four locations. Two of these, the lower Modelo formation of the Santa Monica Mountains and the Monterey formation as represented in quarries at Lompoc, have furnished the largest and best preserved faunas (21 and 39 species, respectively). The third, upper Modelo formation in the Santa Monica mountains presents a smaller number of species (12); here only certain types of small bathypelagic fishes are well preserved; almost all skeletons of other type fish are incomplete and badly fragmented. The fourth locality, Alhambra, is incompletely known, as no planned collecting has ever been under-

taken. It is probably comparable to the upper Modelo formation.

Both lower Modelo of the Santa Monica Mountains and the Lompoc localities seem to represent complete faunal assemblages that were deposited in or near the site of their occurrence. In contrast, the upper Modelo location in the Santa Monica Mountains and most of the scale assemblages seem to represent a selected number of forms that were carried away from the place where the fishes originally lived and died, to be buried at some distance under particular circumstances characteristic of each type of assemblage. These therefore represent death assemblages and not faunal assemblages normally found in any oceanic habitat.

Because of this mode of deposition, chances are limited that great numbers of well preserved scales, shed by fishes dead or alive at some distant location, should arrive at these particular sites. The various scales are not accumulated in such abundance as are most Foraminifera and similar organisms. This makes it necessary to value numerical counts of fish scales in a different manner than customary for samples of Foraminifera. The nomenclature used in describing fish scale abundances is as follows: Scales are considered to be "very abundant," if, for instance, two to four are present on every split surface of a core throughout an interval. Species of herrings, round herrings, or rattails often occur in such abundance. These may occasionally occur in "floods," meaning that entire core surfaces are covered with scales of these species. Most other species may be significant or common members of assemblages occurring with only about four well preserved scales throughout a core section, but they are expected to appear in the same abundance in any other core section taken through the same strata. Rare species are represented by one or two specimens in a normal sample. Other forms may be "very rare"; *Progadus miocenensis*, for instance, was found only once in the whole area. Chances of preservation of scales in general are poor in the uppermost Miocene of this section.

The ecological conditions that must have prevailed at the various localities during deposition were determined according to the total fish assemblages found at each locality. Table 3 lists the bathymetric conditions that seem to be reflected by each assemblage. The age of each locality is determined from the fish assemblages, but in the majority of cases the age is confirmed by age determinations made from foraminiferal assemblages found at the same locality.

The various species are distributed in the different ecological provinces as follows:

Neritic: two species, *Eclipes manni*, and *Bolbocara gyrinus*.

Deep neritic: five species, *Eclipes veternus*, *E. sanctamonicae*, *E. extensus*, *Leptacantholepidus delmontianus*, *L. rotundus*.

Deep neritic to bathyal (or bathypelagic): three species, *Promerluccius venturaensis*, *Progadus pliocenicus*, *Eclipes* sp.

Bathypelagic: three species, *Bregmaceros kreyenehagus*, *Paleobathygadus wilmingtonensis*, *Progadus miocenicus*.

Bathyal: eleven species: *Paleobathygadus yaquinensis*. *P. careagrus*, *P. zemorrianus*, *Probathygadus keaseyensis*, *Promacrurus oregonensis*, *P. alseanus*, *Promacrurus* sp. (three undescribed species), *Pyknolepidus macrospinosus*, *Calilepidus* sp.?

Bathyal to abyssal: five species: *Promacrurus newmanni*, *P. saucesianus*, *Homeocoryphaenoides chiasmacanthus*, *Calilepidus tauxei*, *Oxygoniolepidus washingtonensis*.

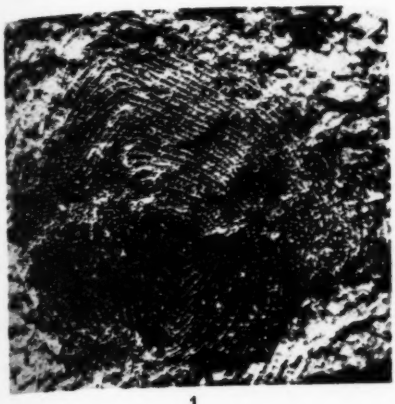
Abyssal: eight species, *Promacrurus zemor-*

EXPLANATION OF PLATE 71

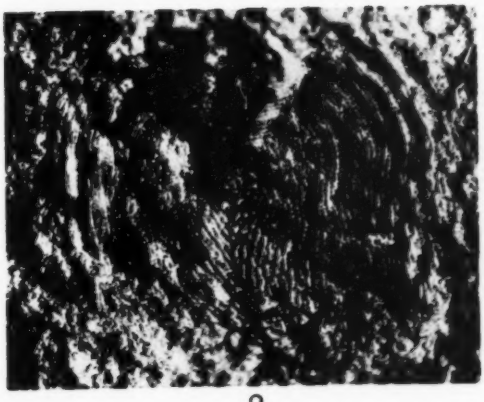
FIG. *1,2*—*Paleobathygadus yaquinensis*, n. sp. *1*, Coarse side of scale from outcrops of Toledo formation in Yaquina Bay area, Oregon. ×24.2 *2*, Smooth side of another scale. ×21.3. (p. 571)

3–5—*Progadus pliocenicus*, n. sp. Oxnard Oil Co. well Vanoni No. 3, at about 5050 ft. depth. *3*, Scale 5 by 4 mm., *4*, Scale 3.76 by 2 mm. *5*, Scale with preserved portion measuring 4 by 3.75 mm. (p. 577)

6—*Progadus miocenicus*, n. sp. Holotype, from Richfield Oil Corp. well Guernsey No. 1, at 5144–5152 ft. depth. Preserved portion of scale 4 by 4.67 mm. (p. 578)



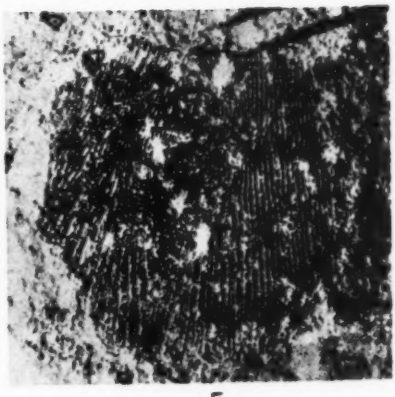
1



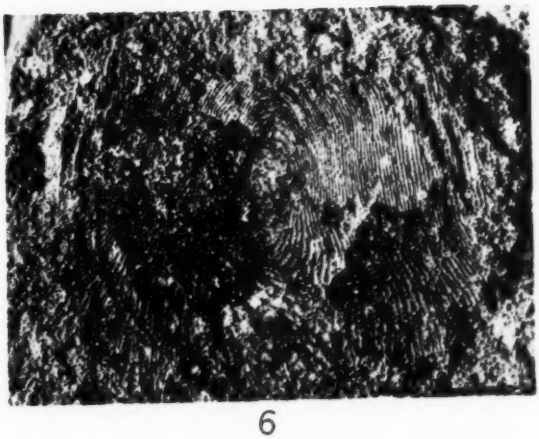
2

3

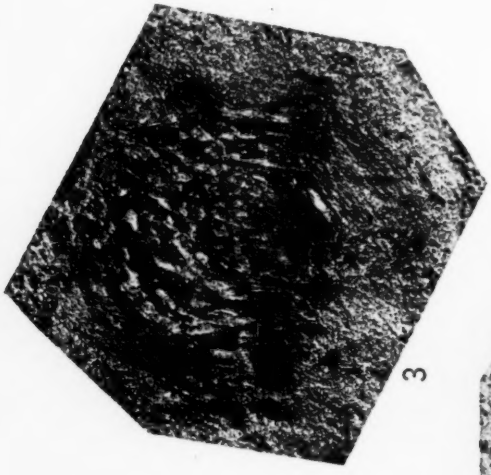
4



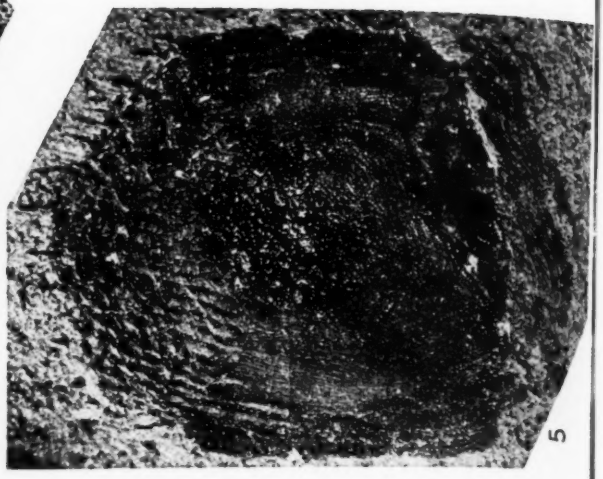
5



6

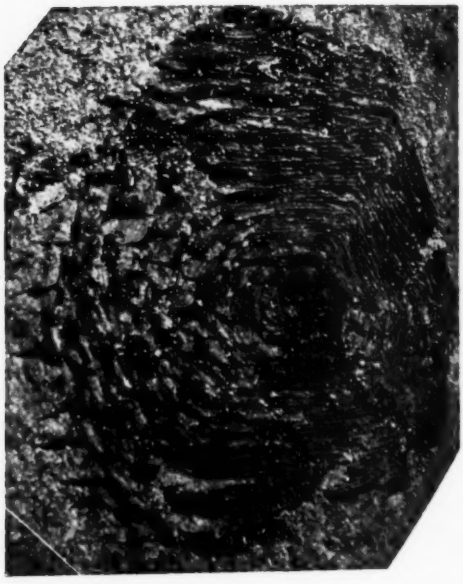


3



5

2



4

1

rianus, P. alferitziensis, P. asymmetricus, P. mimus, Promacrurus sp., *Homeonezumia multispoinsus, Amblygoniolepidus polystichus, Homeomacrurus fernandensis.*

The only criteria on which these ecological determinations are based are the fossil fish assemblages found at the various localities, and their relationships to Recent assemblages. The limiting boundaries of the ecological provinces must necessarily remain arbitrary. By far the majority of the assemblages where anacanthin forms were found fall in the realm of the deep sea, and our knowledge of the ecology of Recent and fossil deep-sea assemblages is notably incomplete.

Sven Ekman (1953) gives a summary review of deep-sea faunas taking into account the results of all major deep-sea expeditions. His comprehensive information furnishes a good basis for the analysis of fossil deposits. He sets a tentative boundary (p. 266–267) between the neritic fauna and the fauna of the slope at 200 to 400 meters in depth. The fauna which has its main distribution below this boundary region is called "deep-sea fauna." Within this latter, two faunistic zones are distinguished: an "upper zone" on the slope from the outer edge of the shelf, containing the archibenthal fauna, and a "lower zone," containing the abyssal fauna. The transitional region between the two is usually roughly placed at the 1000 meter level.

Of the fish groups listed in the fossil faunal assemblages above, the following are considered as endemic elements of the deep sea by Ekman (1953, p. 283–284): The Macruridae (approximately 140 species) are said to be purely archibenthal and abysssal; this is also true for the Bathygadidae, now considered as a subfamily of the Macruridae by many authors; the Halosauridae (20 species) are considered almost wholly abyssal. Among the codfishes (Gadiformes) several genera are completely or preponderantly archibenthal or abyssal in distribution, for instance, *Mora, Antimora,* and *Lepidion.* Bathypelagic forms are discussed separately by Ekman (p. 363–364). *Cyclothone* may occur in an upper zone of the open sea (at about 300 to 500 meter depth) or at a lower zone (500 to 1500 meter depth), depending on the species. The same is probably true for many of the other bathypelagic forms. The following genera listed in the Pacific Tertiary assemblages above, are considered by Ekman to belong to the pelagic deep-water fauna: *Cyclothone, Myctophum, Lampanyctus, Chauliodus, Bathylagus,* and a number of Gadiformes, *Gadiculus, Laemonema,* and *Melanonus.*

The relative percentages in which these bathypelagic forms occur in different areas are discussed by Beebe & Vander Pyl (1944). The graphs showing relative percentages of deep-water myctophids, cyclothones, and "other" bathypelagic fishes taken in the Pacific and Atlantic oceans (p. 60) are of particular interest in this connection. Many well core sections of considerable extent through the uppermost Mohnian and Delmontian of the Los Angeles Basin show faunas of a composition very similar to that given by these authors for the Pacific bathypelagic fauna of today: Myctophids 36.9%, Cyclothons 54.7%, other fishes 8.4%.

Barnhart (1936) reviews the complete fish fauna off California. He lists eight anacanthin species (p. 24–25); these are considered as deep-water forms exclusively

---

EXPLANATION OF PLATE 72

FIG. 1—*Promacrurus alseanus,* n. sp. Holotype, from Yaquina formation, south side of Alsea Bay, Oregon; 4.29 by 5.14 mm. ×9.7. (p. 584)

2—Probably *Promacrurus alseanus,* n. sp. Same locality as fig. 1. ×8.5. (p. 584)

3—*Homeomacrurus fernandensis,* n. sp., from The Texas Co. well Fernando No. 1, at 5510–5520 ft., about 5 by 4.5 mm. (p. 594)

4—*Leptacantholepidus delmontianus,* n. sp. Holotype, from Ohio Oil Co. well Bear State No. 23, at 4434 ft. depth; 3.67+0.25 by 4.67 mm. (p. 592)

5—*Calilepidus tauxei,* n. sp. Holotype, from The Texas Co. well Newman No. 1, at 5800 ft. depth; 6.2+0.40 by 4 mm. (p. 592)

TABLE 2.—LIST OF FAMILIES, GENERA AND SPECIES OF ANACANTHINI, LOCALITIES OF OCCURRENCE AND NUMBER OF SPECIES REPRESENTING EACH FAUNAL ASSEMBLAGE

Family, genus and species	Locality of assemblages	Number of associated species
Bregmacerotidae		
1. *Bregmaceros kreyenhagus* David	Western Gulf Lillis Welch well, California	4–6
Bathygadidae		
2. *Paleobathygadus oligocenicus*, n. sp.	Fred Jasper well, California	?
3. *Paleobathygadus yaquinensis*, n. sp.	Yaquina formation, Oregon	10
	Toledo formation, Oregon	9
4. *Paleobathygadus careagrus*, n. sp.	Texas Careagra well, California	4
5. *Paleobathygadus zemorrianus*, n. sp.	Richfield KCL well, California	4–5
6. *Paleobathygadus wilmingtonensis*, n. sp.	G. P. Terminal well, California	13
7. *Probathygadus keaseyensis*, n. sp.	Keasey formation, Oregon	10
Gadidae		
8. *Eclipes veternus* Jordan & Gilbert	Lower Modelo formation, Santa Monica Mts., California	21
	Alhambra, California	?
9. *Eclipes sanctamonicae* David	Lower Modelo formation, Santa Monica Mts., California	21
10. *Eclipes extensus* Jordan	Alhambra, California	?
11. *Eclipes manni* Jordan	Lompoc, California	39
12. *Eclipes* sp.	Upper Modelo formation, Santa Monica Mts., California	12
13. *Progadus pliocenicus*, n. sp.	Oxnard Vanoni well, California	3–?
14. *Progadus miocenicus*, n. sp.	Richfield Guernsey well, California	14
Macruridae		
15. *Bolbocara gyrinus* Jordan	Lompoc, California	39
16. *Promacrurus zemorrianus*, n. sp.	Texas Pioneer Unit Plan well, Calif.	9
17. *Promacrurus oregonensis*, n. sp.	Yaquina formation, Oregon	10
	Toledo formation, Oregon	9
	Keasey formation, Oregon	10
	Nye formation, Oregon	5
18. *Promacrurus newmani*, n. sp.	Texas Newman well, California	4
19. *Promacrurus alseanus*, n. sp.	Yaquina formation, Oregon	10
20. *Promacrurus alferitziensis*, n. sp.	Standard Alferitz well, California	5
21. *Promacrurus asymmetricus*, n. sp.	Standard Alferitz well, California	5
22. *Promacrurus saucesianus*, n. sp.	Texas Newman well, California	4
23. *Promacrurus mimus*, n. sp.	Amerada Beer well, California	5
	Standard Alferitz well, California	5
24. *Pyknolepidus macrospinosus*, n. sp.	Yaquina formation, Oregon	10
25. *Homeonezumia multispinosus*, n. sp.	Texas Pioneer Unit Plan well, Calif.	9
26. *Amblygoniolepidus polystichus*, n. sp.	Texas Pioneer Unit Plan well, Calif.	9
27. *Oxygoniolepidus washingtonensis*, n. sp.	Arctic section, Washington	6
28. *Homeocoryphaenoides chiasmacanthus*, n. sp.	Texas Newman well, California	4
29. *Calilepidus tauxei*, n. sp.	Texas Newman well, California	4
Calilepidus sp.	Keasey formation, Oregon	10
30. *Leptacantholepidus delmontianus*, n. sp.	Ohio Bear State well, California	8–10
	G. P. Mocco well, California	8–10
31. *Leptacantholepidus rotundus*, n. sp.	Ohio Bear State well, California	8–10
32. *Homeomacrurus fernandensis*, n. sp.	Texas Fernando well, California	3–?
	Texas Towle well, California	3–?
Merlucciidae		
33. *Promerluccius venturaensis*, n. sp.	Oxnard Vanoni well, California	3–?

TABLE 3.—ECOLOGICAL CONDITIONS OF DEPOSITION AT LOCALITIES WHERE ANACANTHIN FISHES WERE FOUND AND AGE OF LOCALITIES

Localities and Anacanthini found	Ecology as determined from faunal lists	Age of localities
Western Gulf Lillis Welch well, at 2099–2100 ft. depth	bathypelagic	upper Eocene
Bregmaceros kreyenhagus		
Fred Jasper well, at 4075–4104 ft. depth		
Paleobathygadus oligocenicus	?	Saucesian or Zemorrian
Yaquina formation, South side of Alsea Bay	bathyal	Zemorrian
Paleobathygadus yaquinensis		
Promacrurus oregonensis		
Promacrurus alseanus		
Pyknolepidus macrospinosus		
Promacrurus sp.		
Toledo formation, Yaquina Bay area	bathyal	Zemorrian
Paleobathygadus yaquinensis		
Promacrurus oregonensis		
Texas Careagra well, at 1427–1447 ft. depth	bathyal	Zemorrian
Paleobathygadus careagrus		
Promacrurus sp.		
Richfield KCL well, at 6443–6452 ft. depth	bathyal	Zemorrian
Paleobathygadus zemorrianus		
G. P. Terminal well, at 5258–5276 ft. depth	bathypelagic	upper Mohnian to Delmontian
Paleobathygadus wilmingtonensis		
Keasey formation, 3000 ft. South of Mist	bathyal	Refugian
Probathygadus keaseyensis		
Promacrurus oregonensis		
Promacrurus sp.		
Calilepidus sp.		
Santa Monica Mts., lower Modelo formation	deep neritic	lower Mohnian
Eclipes santamonicae		
Eclipes veternus		
Santa Monica Mts., upper Modelo formation	deep neritic or bathyal (bathypelagic)	upper Mohnian
Eclipes sp.		
Alhambra, Southern California	deep neritic?	upper Mohnian?
Eclipes veternus		
Eclipes extensus		
Lompoc, California	neritic	Delmontian or uppermost Mohnian
Eclipes manni		
Bolbocara gyrinus		
Oxnard Vanoni well, at 5023–5065 ft. depth	deep neritic to bathyal	lower Pliocene
Progadus pliocenicus		
Promerluccius venturaensis		
Richfield Guernsey well, at 5142–5144 ft. depth	bathypelagic	upper Mohnian or Delmontian
Progadus miocenicus		
Texas Pioneer Unit Plan well, at 5459–6622 ft. depth	abyssal	Zemorrian
Promacrurus zemorrianus		
Homeonezumia multispinosus		
Amblygoniolepidus polystichus		
Nye formation, N. shore of Yaquina bay	bathyal	lower Saucesian to upper Zemorrian
Promacrurus oregonensis		
Promacrurus sp.		
Promacrurus sp.		
Texas Newman well, at 5423–6221 ft. depth	bathyal to abyssal or abyssal	lower Saucesian

TABLE 3—(Continued)

Localities and Anacanthini found	Ecology as determined from faunal lists	Age of localities
Promacrurus newmani *Promacrurus saucesianus* *Homeocoryphaenoides chiasmacanthus* *Calilepidus lauxi*		
Standard Alferitz well, at 1290–1388 ft. depth *Promacrurus alferitziensis* *Promacrurus asymmetricus* *Promacrurus mimus* *Promacrurus* sp.	abyssal	Refugian
Amerada Beer well, at 3540 ft. depth *Promacrurus mimus*	?	Refugian
Arctic section, Washington *Oxygoniolepidus washingtonensis*	bathyal to abyssal	Zemorrian
Ohio Bear State well, at 4212–4434 ft. depth *Leptacantholepidus delmontianus* *Leptacantholepidus rotundus*	deep neritic	upper Mohnian
G. P. Mocco well, at 1775 ft. depth *Leptacantholepidus delmontianus*	deep neritic	Delmontian or upper Mohnian
Texas Towle well, at 4565–4781 ft. depth *Homeomacrurus fernandensis*	abyssal	uppermost Delmontian
Texas Fernando well, at 5510–5625 ft. depth *Homeomacrurus fernandensis*	abyssal	lower Pliocene

with the exception of *Merluccius* which occurs "abundantly in moderate depth."

Gordon Gunter (oral communication) reports on a study of trawl sampling of the level bottom communities of the sea. He finds that Gadiformes even in fairly shallow waters in temperate regions, from about Cape Hatteras northward, are either abundant or dominant on the bottom. The change-over from a gadid-dominated bottom to a sciaenid-dominated bottom coming southward is striking. The Pliocene Ventura Basin locality described above (see under *Progadus pliocenicus* and *Promerluccius venturaensis*) where *Promerluccius* and *Progadus* occur, could have accumulated in temperate water under conditions suggested by this observation. In all other localities considered in this paper the climate was warmer than that of temperate regions.

Based on this summary information and on other specific contributions to our knowledge of the Recent deep-sea fauna (which can not be mentioned in detail in the scope of this paper) the main ecological provinces where Anacanthini were found in the Tertiary deposits of the Pacific Northwest can be briefly characterized as follows:

Neritic environment.—Two anacanthin species occur in Lompoc, Santa Barbara Co., California, a deposit rich in well preserved fish skeletons of upper Mohnian age, which was discussed elsewhere (David, 1943, p. 115–118). Each species of anacanthins is represented by a single specimen only, whereas most of the remaining 37 species of the fauna are represented very abundantly. The two anacanthin forms were evidently not deposited in their normal environment; they are extremely rare and unusual in faunas of this character and have not been found in corresponding assemblages of same age.

Deep neritic environment.—Fish faunas from this environment, all of Mohnian age, are well known from California and have been described previously in some detail: deposits of skeletal material occur in the Santa Monica Modelo formation (David, 1943, p. 1–19); scale assemblages were described from the Gérard-Mohnsprings section and several oil wells of Southern California (David, 1944, p. 34–41). Many other locations could be cited for the Mohnian age, since these faunas occur almost generally in shaly sections of this age throughout California. Anacanthini are again quite rare. Skeletons of *Eclipes* when

they are found, are represented by few specimens; scales of Gadiformes have not yet been found; scales of Macruridae were found in two instances in wells of the San Joaquin Valley, as described above (*Leptacantolepidus delmontianus* and *L. rotundus*).

Pliocene assemblages found in the Ventura Basin may be of neritic or deeper ecology. They are distinguished by the occurrence of a *Merluccius*-like form (hake) of moderate abundance and this may indicate a relationship to Recent assemblages deposited off the California coast, where hakes occur frequently (David, 1947a). The hake is accompanied by a gadiform species. Fish remains are very rare in the Pliocene in general. The Pliocene fauna as a whole is thus hardly known.

Bathypelagic environment.—Two types of assemblages of very different composition belong here. The upper Eocene Kreyenhagen formation presents floods of *Bregmaceros kreyenhagus* in the lowermost portion. This fauna is a peculiar death assemblage uniting forms of the open sea with species of medium depth. It was described elsewhere in detail (David, 1946).

In the upper Mohnian-Delmontian California section a more typical bathypelagic fauna is abundantly found in certain areas of the Los Angeles Basin, as the Wilmington area, the Torrance oil field, where it is best represented, etc. This fauna consists of floods of *Cyclothone* and lantern fish (*Lampanyctus* and *Myctophum*) skeletons, occasional *Chauliodus*, and more frequent *Bathylagus*, represented either as single bones or skeletal parts; scales of lantern fish are represented in floods or as single specimens abundantly. The well known neritic fauna of this age accompanies the bathypelagic elements in the middle to upper Mohnian, where the bathypelagic elements become more and more dominant, while the neritic forms disappear. This fauna was probably deposited beyond the edge of the shelf near the boundary of the neritic and bathyal environments and deposition moved farther and farther away from shore during the uppermost Mohnian and Delmontian. Why fish remains were no longer preserved beyond Delmontian time seems uncertain. A similar fauna, however, mostly represented by skeletal remains, was discussed from the upper Modelo of the Santa Monica Mountains. (David, 1943, p. 51–80). In this locality skeletal fragments of a gadid genus were found, tentatively classified as *Eclipes*.

Only two new species of Anacanthini were described in this report from this environment; both occur in the Wilmington area and are very rare. In both cases the scales were found high in the section where the other fish have ceased to appear in regular abundance. This suggests that deposition was far removed from shore at the time. Elements of the bottom fauna are evidently rarely included in these bathypelagic deposits.

Bathyal environment.—The great majority of Anacanthini described above come from deep-water deposits of Refugian, Zemorrian, Saucesian, or Pliocene age. Some faunules of the California Saucesian and Zemorrian, and one Refugian faunule were illustrated previously (David, 1944, p. 29–30). Faunal lists of other California and various Oregon and Washington locations are given above. These deposits are definitely marked as deep-water environments by the dominance of deep-sea forms. Exact bathymetric zones and distances from shore can be only tentatively determined. Classified as being laid down in the bathyal zone are those assemblages that show a relatively great variety of forms: Bathygadidae, Macruridae, *Beryx*-like forms, lantern fishes and Iniomi occur in varied proportions; *Etringus* and an undescribed clupeid genus are usually present. Abundance and preservation of the clupeoid forms varies, dependent on the distance from shore.

Abyssal environment.—Deposits showing a scarcity of forms, where rattails (Macruridae) are dominant and where hardly any other recognizable fish remains are found, are determined as abyssal. This classification is often substantiated by the presence of *Laytonia*, a genus of the wholly abyssal Halosauridae. The complete absence of any sign of neritic forms in many of these deposits, while at the same time rattails are not only present but abundant, well preserved, and varied, seems to be a quite positive indication that the deposit accumulated at considerable depth. Numerous locations of this type could be listed throughout California lower Saucesian-Zemorrian, and Refu-

gian sections as well as from Oregon and Washington outcrops of that age. Sections of Zemorrian to lower Saucesian age generally present well preserved fish remains in their shaly portions, most often of bathyal and abyssal character. However, shallow, warm water facies of neritic character are known also from the Zemorrian of California. In assemblages of this type, deep-water forms are absent; characteristic forms are certain groupers, and a genus related to the salmonid genus *Leucichthys* (illustrated in David 1947a, fig. 2, No. 9, 11; fig. 3, no. 1). Porgies, rockcods, mackerels, and floods of *Etringus* are common. Such faunas were found in the Texas Careagra No. 1 at the interval 1168 to 1447 ft., higher in the section than where the deep-water facies occurs; in many wells of Santa Barbara Co.; in the Richfield San Marcus wells and in other wells of the area. No Anacanthini occur in these neritic Zemorrian facies; they are mentioned here only to show that the neritic assemblages of this age exist and are clearly distinguished from the deep-water facies, and present abundances of the neritic forms that occur so sparingly in the deep water faunas described.

Another typical abyssal fauna is found in the uppermost Delmontian and lower Pliocene (Pico formation) in the Hasley Canyon section of California. In the Pliocene, fish remains in general are rarely found. The Hasley Canyon section, in the Castaic area, so far is the only location where this fauna is known (see above under *Homeomacrurus fernandensis*).

The ecologic distribution of the Pacific coast Tertiary Anacanthini (particularly the Macruridae), almost entirely in deep-water deposits, does not conform with Weiler's view (1949) that this group of fishes inhabited shallower water during that period. Descriptions of Tertiary Macruridae show that they were as highly specialized as they are today. The scales described here show great variety and specialization similar to that known from the Recent fauna. It is very unlikely therefore that the group underwent a fundamental change in habitat from Tertiary to Recent time. While Weiler feels that some of the European macrurid occurrences could be explained by mixing of forms near the bottom of steep slopes, he feels this does not hold true for those assemblages based on otolith occurrences. It seems that investigation of the particular circumstances which permit deposition and preservation of fish otoliths may furnish an explanation for the discrepancies in macrurid Tertiary occurrences.

Paleoecological Considerations

The above given descriptions of the environments of the fossil sites where Anacanthini occur are mainly based on our knowledge of Recent marine ecology. Bathymetric determinations were made "statistically," using amount and preservation, and admixture of the elements from different environments of the living sea deposited in each fossil locality. Another important factor in determining the true ecologic significance of these sites is consideration of sedimentary conditions leading to deposition. We must realize that fossil faunas represent death assemblages rather than life assemblages. The paleoecologic term "facies" stands for a deposit that unites organisms many of which had been dead a long time before they were buried.

Deposits of fish remains in Recent oceanic sediments have rarely been studied. The only well known location has been described by Brongersma-Sanders (1948). This is located on the sea floor of the azoic zone near Walvis Bay, Southwest Africa, between latitudes 21° 30′ and 24° 30′, 25 to 30 miles west of the coastline and 77 to 84 fathoms deep. It is characterized by its high organic content, presence of H_2S, diatom ooze, abundance of fish remains, and great scarcity of remains of benthonic invertebrates. The existence of this deposit and similar deposits is explained as the result of a number of factors working together, such as periodic upwelling of water causing high organic production, resulting in mass production of plankton. This, owing to noxiousness, causes mass mortalities of fishes as well as benthonic invertebrates. Decomposition can not keep up with supply. Only anaerobic bacteria can exist. Fish sinking into these sediments have a good chance for preservation. Brongersma-Sanders lists fish forms found dead on the beach nearby, mostly consisting of neritic forms, but she does not evaluate fish material actually

found in the deposit. Brongersma-Sanders (1949) gives a review of literature reporting the occurrence of fish remains in Recent deposits. The rarity of fish remains in most marine deposits is striking. Where present, they occur under conditions probably similar to Walvis Bay, either near coasts or sometimes in fairly deep water. None of the occurrences listed seem to show faunal similarities to the sites described in this report. David (1947a) describes fish remains (scales, bones, teeth) found in dredge samples from the Catalina Channel, off the coast of Southern California. The samples were taken at varying depth near shore. Scales of *Merluccius* were found in all samples that contained fish remains, at 192 to 758 meters depth. A gadoid form related to *Bathygadus* was found at 758 meters depth. Bathypelagic forms, as two species of lantern fishes and an Iniomi occurred in samples from 518 to 758 meters depth, the latter being the deepest location from which samples were taken. Fish scales of neritic forms were found during a brief investigation in H_2S rich muds dredged off the coast of Woods Hole, Mass.

The above-mentioned occurrences of *Merluccius* and *?Bathygadus* seem to be the only ones known where Anacanthini were found in Recent sediments.

Brongersma-Sanders (1948) stresses the similarities of the deposits of Walvis Bay with the California bituminous and siliceous fish shales. Of the California locations described above, the Modelo formation of the Santa Monica Mountains, and Lompoc seem closest to the Walvis Bay characteristics. Neritic faunas are found in both localities, and complete skeletons are preserved in some sites of both areas. None of the other locations described here equal Walvis Bay in both bathymetric and sedimentary conditions. Some of the deposits are very sandy. State of preservation and fragmentation of some of the scales indicate that they have been moved over long distances before deposition. Particularly the scales of the Saucesian-Zemorrian *Etringus* which are very abundant in most deposits of that age, show a varied preservation. While usually well preserved and complete in deposits thought to be neritic, they show an increasing abrasion and fragmentation in deposits rich in deep-water forms. Length of time and distances that fish scales, after being removed from the fish body, may travel suspended in the ocean and carried by currents, have never been studied. The European locations discussed by Weiler (1949) where macrurid otoliths were found among otoliths of forms from a diversity of habitats, again, seem to depend on completely different and unknown conditions of deposition.

Altogether, from the meager information available on burial and deposition of fish remains, it does not seem possible to determine how far from shore the anacanthin locations may have been. Kuenen (1950, p. 316–24) differentiates between the following environments of marine sedimentation that may be of interest here: pelagic-abyssal environment, coastal distance at least several hundred kilometers, depth greater than 1000 meters; hemipelagic-abyssal environment, coastal distance less than several hundred kilometers, depth greater than 1000 meters; bathyal environment, coastal distance normally a few dozen to a few hundred kilometers, depth 200 to 1000 meters; neritic environment coastal distance seldom more than a few hundred kilometers, depth from low tide to 200 meters; euxinic environment, depth varying, characterized by poor ventilation of bottom water, resulting in absence of bottom fauna. (At present euxinic conditions are said to have developed in basins of varying depth, such as the Norwegian fjords and the Black Sea!)

Of the Pacific coast anacanthin localities, none is likely to fall into the pelagic-abyssal environment, since all sediments show great amounts of organic matter, a variety of composition, and some evidence of coastal influence. Even in localities that present an almost exclusively abyssal assemblage (such as portions of the Saucesian of the Texas Company Newman well No. 1 and the Texas Company Pioneer Unit Plan well No. 1) very sandy strata are present. These localities that present abyssal fish remains may have accumulated in the hemipelagic-abyssal environment, or, more likely, in the deepest portions of the bathyal as defined by Kuenen. Most of the anacanthin localities present a high organic content, silt or mud-

stones, or siliceous shales and conform best with the bathyal or a deep-water euxinic environment.

Age of Assemblages

Anaçanthin forms do not occur throughout the entire stratigraphic section of the Pacific coast Tertiary, but are shown in Table 3 to be distributed through the stages as follows:

Lower Pliocene: Three species, *Progadus pliocenicus, Homeomacrurus fernandensis, Promerluccius venturaensis.*

Delmontian or uppermost Mohnian: Five species, *Eclipes manni, Paleobathygadus wilmingtonensis, Progadus miocenicus, Bolbocara gyrinus, Leptacantholepidus delmontianus.*

Mohnian: Five species, *Eclipes veternus, E. extensus, E. santa-monicae, Leptacantholepidus delmontianus, L. rotundus.*

Luisian and Relizian: None. No Anacanthini have been found in either the Luisian or Relizian stage. These two stages present well preserved abundant fish remains, mostly of a shallow water neritic facies of warmer water than present in the Mohnian. These faunas have been described very incompletely so far (David, 1944, p. 34; in David, 1947b, some of these scales are illustrated in fig. 2, nos. 5,6,7,8).

Saucesian or Saucesian-Zemorrian: Eight species, *Paleobathygadus oligocenicus, Promacrurus oregonensis, P. newani, P. saucesianicus, Promacrurus* sp. (two species), *Homeocoryphaenoides chiasmacanthus, Calilepidus tauxi.*

Zemorrian: Ten species, *Paleobathygadus yaquinensis, P. zemorrianus, P. careagrus, Promacrurus oregonensis, P. alseanus, P. zemorrianus, Pyknolepidus macrospinosus, Homeonezumia multispinosus, Amblygoniolepidus polystichus, Oxygoniolepidus washingtonensis.*

Refugian: Eight species, *Probathygadus keaseyensis, Promacrurus alferitziensis, P. oregonensis, P. asymmetricus, P. mimus, Promacrurus* sp. (two species), *Calilepidus* sp.

Upper Eocene: One species: *Bregmaceros kreyenhagus.*

In short, the greatest abundance and variety of Anachanthini are found in the Refugian, Zemorrian to lower Saucesian stages. A variety of forms usually appearing in small numbers is found in the upper Mohnian to Delmontian. In the lower Pliocene, Anacanthini are again more abundant. None is found in the middle stages Luisian and Relizian.

The ecological characterization of the California Tertiary stages by Kleinpell (1938), based on Foraminifera, agrees remarkably well with the distribution of the Anacanthini. The eight stages are roughly divided into three groups. The lower stages, Refugian, Zemorrian and Saucesian, show great bathymetric diversities. The middle stages are characterized by uniform faunal and lithologic facies dominated by medium depth faunas. The upper stages, Mohnian, Delmontian, and lower Pliocene, resemble the lower stages in most respects. Particularly the Refugian and Zemorrian are said to be rich in abyssal foraminiferal genera as *Gyrodina* and *Cyclamina.* These are still common and characteristic in the Saucesian, but become scarce in the overlying Relizian. In the Mohnian, types characteristic of the neritic zone are common; deep-water forms such as *Gyrodina* again become locally common, particularly in the upper Mohnian, but are not characteristic for the stage. Ecologic diversity again is noted in the Delmontian, where abyssal faunules are common in the Los Angeles Basin, and in Southern California the Delmontian is rich in open sea types, as represented by *Globigerina.* The lower Pliocene foraminiferal faunules resemble those of the Zemorrian in ecological diversity.

This ecologic characterization of the foraminiferal faunas is well coordinated with the stage distribution of the Anacanthini, a class of almost entirely deep-water forms, as follows: their greatest abundance and variety in the Refugian, Zemorrian, and lower Saucesian, their absence in the Relizian and Luisian; their reappearance as occasional elements in the otherwise neritic lower Mohnian, and their increasing variety in the uppermost Mohnian and Delmontian bathypelagic fauna, which is remarkably rich in (non-anacanthin) open sea forms in the Los Angeles Basin; and again their greater abundance in the lower Pliocene.

REFERENCES

ARAMBOURG, CAMILLE, 1925, Révision des poissons fossiles de Licata (Sicile): Annales de paléontologie, vol. 14, p. 39–96.

——, 1927, Les poissons fossiles d'Oran: Matériaux Carte Géologie Algérie Paléontologie, ser. 1, no. 6, p. 1–298, 46 pl.

BARNARD, K. H., 1925, 1927, A monograph of the marine fishes of South Africa: Annals South African Mus., vol. 21, pt. I–II, 1065 p., 37 pl.

BARNHART, P. S., 1936, Marine fishes of Southern California: Univ. California Press, Berkeley, 214 p.

BEEBE, WILLIAM, & VANDER PYL, MARY, 1944, Eastern Pacific Expeditions of the New York Zoological Society. XXXIII. Pacific Myctophidae (Fishes): Zoologica, Sci. Contr. New York Zool. Soc., vol. 29, p. 59–80.

BELLOC, G., 1929, Etude monographique du Merlu, *Merluccius:* Rev. travaux Office Sci. Tech. Pêches Maritimes, vol. 2, p. 153–99.

BRONGERSMA-SANDERS, MARGARETHA, 1948, The importance of upwelling water to vertebrate paleontology and oil geology: Konink. Ned. Akad. Wetensch. Naturk. Verh., ser. 2, vol. 45, p. 1–112.

——, 1949, On the occurrence of fish-remains in fossil and Recent marine deposits: Bijdragen Dierk., vol. 28, p. 65–76.

COCKERELL, T. D. A., 1911, Some notes on fish scales: Biol. Soc. Washington Proc., vol. 24, p. 209–13.

——, 1912, (1913) Observations on fish scales: U. S. Bur. Fisheries Bull., vol. 32, p. 119–174.

DAVID, L. R., 1943, Miocene fishes of Southern California: Geol. Soc. Am., Special Paper 43, 193 p.

——, 1944, Use of fossil fish scales in Micropaleontology: Contr. Paleont., Carnegie Inst. Washington Pub. 551, no. 3, p. 25–44.

——, 1946, Some typical Eogene fish scales from California: Contr. Paleont., Carnegie Inst. Washington Pub. 551, no. 4, p. 45–80.

——, 1947a, Recent fish scales deposited off the California Coast: Am. Assoc. Petrol. Geol., Bull., vol. 31, p. 367–370.

——, 1947b, Use of fossil fish scales in the stratigraphy of the Pacific Coast: Petroleum Engineer, May, p. 104–113.

——, 1948, Halosauridae from the California Tertiary: Jour. Paleont., vol. 22, no. 1, p. 94–100.

EKMAN, SVEN, 1953, Zoogeography of the Sea (Translated from the Swedish by Elizabeth Palmer): Sidgwick and Jackson, London, p. 543

ERASMO, G. D', 1927–1929, L'Ittiofauna fossile di Racalmuto Sicilia: Giorn. Soc. Sci. Nat. Econom., Palermo, vol. 35, pt. I–III, p. 73–106, fig. 1–9.

——, 1929, L'iittiofauna fossile di Sénegallia: Atti. Accad. Sci. fis. mat., Napoli, vol. 18, p. 1–84, fig. 1–4.

——, 1930, L'Ittiofauna fossile del Gabbro: ibid., vol. 18, ser. 2, no. 6, p. 1–118.

GARMAN, S., 1899, Deep sea fishes: Mus. Comp. Zool. Harvard Univ. Mem., vol. 24, p. 1–431.

GILBERT, C. H., & HUBBS, C. L., 1916, Report on the Japanese macrourid fishes: U. S. Nat. Mus. Proc., vol. 51, p. 135–214.

——, 1920, The macrourid fishes of the Phillipine Islands and the East-Indies: U. S. Nat. Mus. Bull., vol. 51, p. 135–214.

HART, T. J., 1948, Distribution and biology of the hakes: Cambridge Phil. Soc., Biol. Rev., vol. 23, p. 62–80.

JORDAN, D. S., 1921, The fish fauna of the California Tertiary: Stanford Univ. Pub., Biol. Sci., vol. 1, p. 235–300, 47 pl.

——, 1925, The fossil fishes of the Miocene of Southern California: Stanford Univ. Pub., Biol. Sci., vol. 4, p. 1–51, 21 pl.

——, & GILBERT, J. Z., 1919, Fossil fishes of Southern California: Stanford Univ. Pub., p. 1–98.

——, ——, 1920, Fossil Fishes of the Diatom beds of Lompoc, California: Stanford Univ. Pub., p. 1–45.

Kleinpell, R. M., 1938, Miocene Stratigraphy of California, Am. Assoc. Petroleum Geologists, Tulsa, Oklahoma, 540 pp.

KUENEN, PHILIP H., 1950, Marine Geology: John Wiley, New York, 576 p.

LONGLEY, W. H., & HILDEBRAND, S. F., 1941, Systematic catalogue of the fishes of Tortugas, Florida: Papers Tortugas Lab., vol. 34, p. 1–331.

PARR, A. E., 1946, The Macrouridae of the western North Atlantic and Central American seas: Bingham Oceanograph Coll. Bull., vol. 10, no. 1, p. 1–99.

PEABODY, E. B., 1931, Scales of fishes of the order Anacanthini: Univ. Colorado Studies, vol. 18, p. 133–50.

PIERAGNOLI, L., 1919, Otolithi Pliocenici della Toscana: Riv. Ital Paleontol., vol. 25, Parma, p. 21–44.

SCHUBERT, R. J., 1905–06, Die Fisch-Otolithen des Oesterreich-ungarischen Tertiärs. I–III: Jahrb. K. geol. Reichsanstalt, Wien, vol. 55, p. 613–38; vol. 56, p. 623.

——, 1912, Die Fisch-Otolithen der ungarischen tertiären Ablagerungen: Mitt. Jahrb. ungar. geol. Reichsanstalt, Budapest, p. 115–39.

SMITH, H. M., & RADCLIFFE, L., 1912, Philippine fishes from the Albatross expedition: U. S. Nat. Mus. Proc., vol. 43, p. 105–140.

WEBER, MAX, 1913, Fische der Siboga Expedition: E. J. Brih, Leiden, 710 p.

WEILER, WILHELM, 1942, Die Otolithen des Rheinischen und nord west deutschen Tertiärs: Prussia, Geolog. Landesanstalt Abh., Berlin, Neue Folge, Heft 206, p. 1–140, 14 pl.

——, 1949, Die Otolithen aus dem Jungtertiär Süd-Rumänians. 1) Buglow und Sarmatian: Senckenbergiana, vol. 26, p. 1–3, 87–115; ibid., vol. 30, p. 291–93.

MANUSCRIPT RECEIVED JUNE 15, 1954

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 608–610, PL. 73, MAY 1956

THE TYPE SPECIES OF *LITOCEPHALUS* RESSER, 1937 (TRILOBITA)[1]

ALLISON R. PALMER
U. S. Geological Survey, Washington, D. C.

ABSTRACT—A cranidium of an Upper Cambrian trilobite described as *Dicellocephalus richmondensis* by Walcott, 1884 (type species of *Litocephalus* Resser, 1937) and a pygidium described as *Dikellocephalus bilobatus* by Hall & Whitfield, 1877 (type species of *Pterocephalina* Resser, 1938) are here described as parts of the same trilobite. *Litocephalus bilobatus* (Hall & Whitfield).

THE type species of *Litocephalus* (Resser, 1937, p. 17) was designated as *Dicellocephalus richmondensis* Walcott from USGS locality 60 (OS) in the Dunderberg shale of Late Cambrian age, Eureka district, Nevada. The holotype, a nearly complete but almost wholly exfoliated cranidium, is in a dense, fine-grained gray limestone with no other associated trilobite parts. Many cranidia from USGS locality 1297 (CO), also from the Dunderberg shale in the Eureka distict, seem to be conspecific with *D. richmondensis* Walcott. These cranidia are associated with pygidia, a few free cheeks and hypostomes, and scraps of thoracic segments, all of which are probably parts of the same trilobite. An articulated trilobite with a similar association of parts is present at USGS locality 1674 (CO) from the Hales limestone of Late Cambrian age in the Tybo district, Nevada.

The pygidia from USGS locality 1297 (CO) have a distinctive median notch in the posterior margin and confrom in all characteristics to *Dikellocephalus bilobatus* Hall & Whitfield, another species from the Dunderberg shale in the Eureka district. This species was designated by Resser (1938, p. 42) as the type species of *Pterocephalina*.

The trilobite represented by disarticulated parts at USGS locality 1297 (CO) thus has its cranidium and pygidium presently assigned to two different species, each of which is the type species of a genus. Because Hall & Whitfield described *D. bilobatus* for the pygidium in 1877, seven years before Walcott (1884, p. 41) described *D. richmondensis* for the cranidium, the correct trivial name for the trilobite is *bilobatus*. *Litocephalus* is the oldest of the two generic designations. The present binomial designation of this trilobite, which is the type species of *Litocephalus*, is thus *Litocephalus bilobatus* (Hall & Whitfield).

A description of *L. bilobatus* (Hall & Whitfield) based on material from USGS locality 1297 (CO) and supplemented by information derived from the complete carapace of *Litocephalus* sp. from the Tybo district, is presented below.

Genus LITOCEPHALUS Resser

Litocephalus RESSER, 1937, p. 17.
Pterocephalina RESSER, 1938, p. 42.

Type species.—*Dicellocephalus richmondensis* Walcott, 1884, p. 41, pl. 10, fig. 7 (= *Dikellocephalus bilobatus* Hall & Whitfield, 1877, p. 226, pl. 2, fig. 36).

Diagnosis.—Cephalon with well-defined convex border on cranidium and free cheeks, and a median node on occipital ring. Thorax with tips of pleurae extended into long, slender, backward directed spines. Pygidium with border concave; posterior margin with deep median notch reaching nearly to posterior end of axial lobe.

Discussion.—With the exception of *Dikellocephalus bilobatus* Hall & Whitfield, neither the species assigned to *Pterocephalina* by Resser (1942, p. 76–79) (*P. grata*, *P. notha*, *P. pogonipensis*, *P. texana*, and *P. utahensis*) nor *Pterocephalina* cf. *P. grata* Resser (Wilson, 1954, p. 271) are assignable to *Litocephalus*. Other generic designations of these species must await a comprehensive study that is beyond the scope of this paper.

LITOCEPHALUS BILOBATUS (Hall & Whitfield)

Pl. 73, fig. 1–6,8

Dikellocephalus bilobatus HALL & WHITFIELD, 1877, p. 226, pl. 2, fig. 36.

[1] Publication authorized by the Director, U. S. Geological Survey.

Dicellocephalus richmondensis WALCOTT, 1884, p. 41, pl. 10, fig. 7.
Litocephalus richmondensis (Walcott). RESSER, 1937, p. 17.
Pterocephalina bilobata (Hall & Whitfield). RESSER, 1938, p. 42; 1942, p. 77, pl. 14, fig. 39–43.

Description.—Carapace elongate subovate in outline; widest about on line through occipital ring. Cephalon subsemicircular in outline with prominent posteriorly directed genal spines. Tips of thoracic pleurae long, extended posteriorly behind pygidium

Cranidium, exclusive of posterior limbs, elongate rectangular in outline, moderately arched transversely and longitudinally, moderately to strongly rounded at anterior margin. Glabella distinct, well defined, straight sided, tapered slightly forward, bluntly rounded or truncate anteriorly; commonly featureless although traces of three pairs of slightly arcuate glabellar furrows may be seen on exfoliated specimens. Dorsal furrows deepest along sides and at anterolateral corners of glabella, shallow on midline. Occipital ring with small median node. Occipital furrow narrow and shallow on median line; broadens and deepens laterally; extends nearly to dorsal furrow. Brim and border present, separated by a narrow marginal furrow. Brim flat. Border in profile arched up sharply from marginal furrow, then gently arched to anterior margin; length (saggital) about three-fourths that of brim, greatest on midline. Fixed cheeks nearly flat, slightly upsloping; width about one-third that of glabella at occipital ring. Palpebral lobes slightly arcuate, situated opposite middle third of glabella. Palpebral furrow shallow. Ocular ridges present but poorly defined. Posterior limbs narrow, sharp-pointed; length (transverse) about equal to width of glabella at occipital furrow.

Facial sutures diverge slightly forward from palpebral lobes until reaching marginal furrow, then turn sharply inward to cut anterior margin almost directly in front of anterolateral corners of glabella. Posterior course of facial suture widely divergent behind palpebral lobes; continues in straight line until across marginal furrow where it turns sharply backward to cut posterior margin well within genal angle.

Hypostome elongate subovate in outline, strongly arched transversely and longitudinally. Anterolateral corners extended into short depressed pointed alae. Border narrow, distinct, present only along sides. Central body not clearly differentiated from posterior portion of hypostome.

Free cheek with long, slender, sharply pointed anterior projection resulting from partly intramarginal anterior course of facial suture. Border separated from ocular platform by narrow marginal furrow; profile similar to that on border of cranidium. Lateral and posterior marginal furrows of about equal depth; they join at genal angle and extend for a short distance onto genal spine as a shallow, pointed depression. Infraocular ring present between eye surface and ocular platform.

Thorax probably composed of 13 segments (see specimen from Tybo district, Pl. 1, fig. 7). Axial lobe distinct, elevated above nearly flat pleural lobes. Pleural furrow of each segment broad, shallow, located at or slightly anterior to midlength (exsaggital) of segment, not extended to thoracic tip. Tips on all but perhaps last two thoracic segments long, slender, turned sharply backward from proximal portion of pleuron; length about equal to width (transverse) of proximal portion.

Pygidium wide, short, much smaller than cephalon. Axial lobe prominent, elevated above pleural platforms; four or five distinct axial rings and a bluntly pointed terminal portion present; posterior margin of first segment distinctly separated on medial line from fused portion of articulating half-ring of second segment. Pleural platforms gently arched, downsloping; broad, shallow pleural furrows of four or five segments present, extending nearly across border. Shallow, narrow interpleural grooves visible only between first and second segments. Border slightly concave, greatest width about equal to that of pleural platform; inner margin marked by narrow, shallow, straight furrow extending from tip of axial lobe to anterolateral corner of pygidium; lateral margin a broad curve extending from anterolateral corner of pygidium to base of prominent posterior medial notch near tip of axial lobe.

Surfaces of all parts of carapace apparently smooth.

Complete specimens may have been a

much as 85 mm. long, based on comparisons of the sizes of the largest pygidia and cranidia from the Eureka district and the complete carapace from the Tybo district.

Discussion.—The combination of characteristics described above is unlike that of any other described trilobite. The most closely related described form is *Labiostria convexiimarginatus* Palmer (1954, p. 751) from the *Aphelaspis* zone of the Riley formation in central Texas. This species lacks the long tips to the thoracic pleurae and the prominent median notch in the posterior margin of the pygidium that are most characteristic of *Litocephalus bilobatus* (Hall & Whitfield).

Litocephalus bilobatus (Hall & Whitfield) is associated in the Eureka district with other trilobites that occur in or immediately below the *Elvinia* zone.

The apparent differences between the holotype cranidium of *D. richmondensis* Walcott (Pl. 73, fig. 1) and the cranidium figured here as *Litocephalus bilobatus* (Hall & Whitfield) (Pl. 73, fig. 4) are due entirely to size. The holotype of *D. richmondensis* is an exceptionally large cranidium. Large cranidia of *L. bilobatus* at USGS locality 1297 (CO) are essentially identical to the holotype of *D. richmondensis*.

Although the articulated specimen from the Tybo district has an imperfectly preserved and somewhat crushed cephalon, it is certainly congeneric with *L. bilobatus*. The tips of the thoracic pleurae are about twice as long as those of *L. bilobatus* and this may constitute a valid specific distinction. Until more articulated specimens can be collected, however, and infraspecific variation in the length of the thoracic tips ascertained, such a distinction cannot be adequately demonstrated.

Figured specimens and occurrence.—Cranidium, holotype of *Dicellocephalus richmondensis* Walcott, USGS loc. 60 (OS) opposite dump of Richmond mine, USNM 24616; pygidium, holotype of *Dikellocephalus bilobatus* Hall & Whitfield, USGS loc. 65 (OS) Sierra canyon, USNM 24568; cranidium, USGS loc. 1297 east side of Sierra canyon, USNM 128324a; free cheek, same loc., USNM 128324b; hypostome, same loc., USNM 128324c; thoracic segment, same loc., USNM 128324d; pygidium, same loc., USNM 128324e; all from the upper part of the Dunderberg shale, Eureka district, Nevada. Complete carapace, USGS loc. 1674 north side of canyon, above Hales mine, USNM 128325; lower part of Hales limestone, Tybo district, Nevada.

REFERENCES

HALL, JAMES, & WHITFIELD, R. P., 1877, Fossils of the Potsdam Group: U. S. Geol. Expl. 40th Par. Rept., vol. 4, p. 205–232, pl. 1, 2.

PALMER, A. R., 1954, The faunas of the Riley formation in central Texas: Jour. Paleont., vol. 28, no. 6, p. 709–786.

RESSER, C. E., 1937, Third contribution to nomenclature of Cambrian trilobites: Smithsonian Misc. Coll., vol. 95, no. 22, 29 p.

——, 1938, Fourth contribution to nomenclature of Cambrian fossils: Smithsonian Misc. Coll., vol. 97, no. 10, 43 p.

——, 1942, New Upper Cambrian trilobites: Smithsonian Misc. Coll., vol. 103, no. 5, 136 p.

WALCOTT, C. D., 1884, Paleontology of the Eureka district: U. S. Geol. Survey Mon. 8, p. 1-64.

WILSON, J. L., 1954, Late Cambrian and early Ordovician trilobites from the Marathon uplift, Texas: Jour. Paleont., vol. 28, no. 3, p. 249–285.

MANUSCRIPT RECEIVED OCTOBER 28, 1955

EXPLANATION OF PLATE 73

All figures are stereophotographs

FIG. *1*—*Dicellocephalus richmondensis* Walcott, ×1. Holotype cranidium, USNM 24616, USGS locality 60 (OS), Dunderberg shale, Eureka District, Nevada.

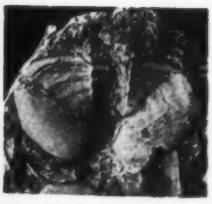
2—*Dikellocephalus bilobatus* Hall & Whitfield, ×1. Holotype pygidium, USNM 24568, USGS locality 65 (OS), Dunderberg shale, Eureka district, Nevada.

3-6,8—*Litocephalus bilobatus* (Hall & Whitfield,) ×2. *3*, Thoracic segment, right pleural lobe; *4*, cranidium; *5*, rubber cast of internal mold of pygidium; *6*, hypostome, *8*, left free cheek. All USNM 128324, from USGS locality 1297 (CO), Dunderberg shale, Eureka District, Nevada.

7—*Litocephalus* sp., ×2. Partly weathered complete carapace, USNM 128325, USGS locality 1674 (CO), Hales limestone, Tybo district, Nevada.

1

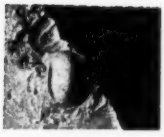
2



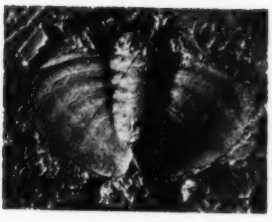
3

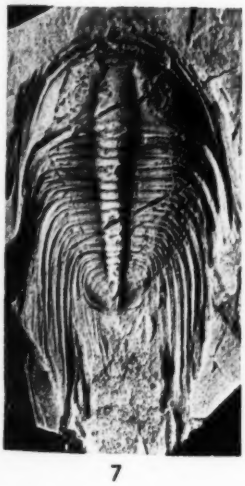
4

5

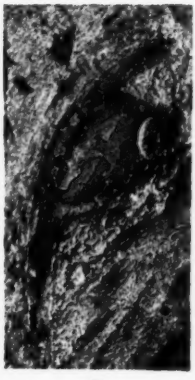


6

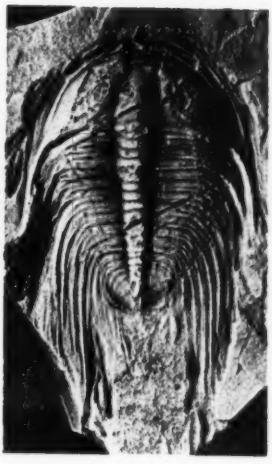




7



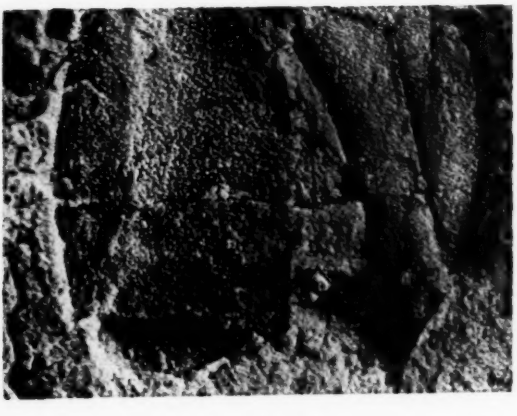
8



1

2

3



4

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 611–614, PL. 74. 2 TEXT-FIG., MAY 1956

MICROSTRUCTURE OF THE PLATES IN THE CARPOID ECHINODERM *PARANACYSTIS*

KENNETH E. CASTER AND THEODORE H. EATON, JR.
University of Cincinnati and East Carolina College

ABSTRACT—Study of the microstructure of the plates of the Lower Devonian carpoid *Paranacystis* from Paraná, Brazil, indicates that they were penetrated by a labyrinth of fine canals which continued from plate to plate and opened on the outer surface in minute pores. The structure is similar to that described in the outer layer of plates of the ostracoderm *Procephalaspis oeselensis*. It is suggested that, if the carpoids and ostracoderms are directly related, it is possible the canals originally functioning in respiration eventually came to possess sensory receptors.

DETAILED study of plate structure in the recently described Brazilian carpoid, *Paranacystis petrii* Caster, 1954, (Pl. 74) reveals some important points of similarity to that of certain ostracoderm fishes. Although the rough outward resemblance in form and plate arrangement between selected carpoids and ostracoderms has been noted (Gregory, 1935, 1936, 1946, 1951), it has not been possible to make any comparison of microscopic details because of the want of adequate carpoid material. Denison (1947, 1951) and others have provided abundant information on ostracoderm plate structure. The holotype of *Paranacystis petrii* now shows an extraordinary system of plate-canals not previously seen in the carpoids.

Paranacystis occurs in the Lower Devonian Ponta Grossa shale, Paraná, and the hypodigm of the present species is the property of the Geological Museum, University of São Paulo, Brazil. The holotype consists of two external molds on separate pieces of silty shale, showing the dorsal and ventral surfaces of the same specimen, with a small portion of the plate structure still present, viewed, therefore, in its internal aspect. The general matrix is pinkish, with limonite granules, but certain features, including casts of the canals, are of a contrasting white material. This is not lime, as had been supposed in the original description (Caster, 1954, p. 128). Grinding to thin sections was out of the question because of the lack of duplicates and the fragility of the specimens. Nevertheless direct examination brought out the features adequately.

Surface topography of the plates of theca and peduncle is shown, in reverse, by the impression which they made in the sediment (Pl. 74; Text-fig. 1), with relatively little crushing indicated. The shale is sufficiently fine-grained to represent clearly the smallest depressions and tubercles, on the order of 0.02 to 0.05 mm. in height or width. The original calcareous matrix of the plates themselves is, of course, completely lacking, but in place of it, in certain areas, there is a reddish granular material occupy-

EXPLANATION OF PLATE 74

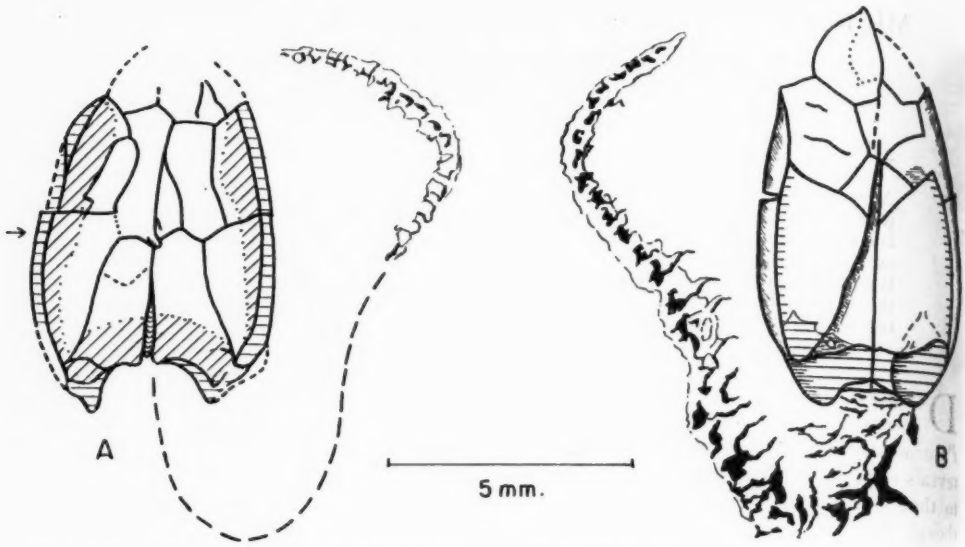
Paranacystis petrii Caster. Details of specimens from the Lower Devonian (Ponta Grossa shale) of the State of Paraná, Brazil.

FIG. *1*—Holotype. External mold of the superior (carapace) surface; note the molds of pore openings covering the exterior. For other details see Caster, 1954. From Lange Collection, Dept. Geol. and Paleont., Univ. São Paulo, Brazil; no. 177B.

2—Holotype. External mold of the inferior (plastron) surface; enlargement shown in fig. 3, below, came from patch of white on left margin of the specimen.

3—Enlargement of portion of a marginal plate, revealing fillings of the canal system which permeates the originally calcareous plates in a labyrinth. Approx. ×25.

4—Detail of a paratype, showing transverse furrow. Museu Paranaense (Curiteba), no. 1/22,10. From Lange Collection.

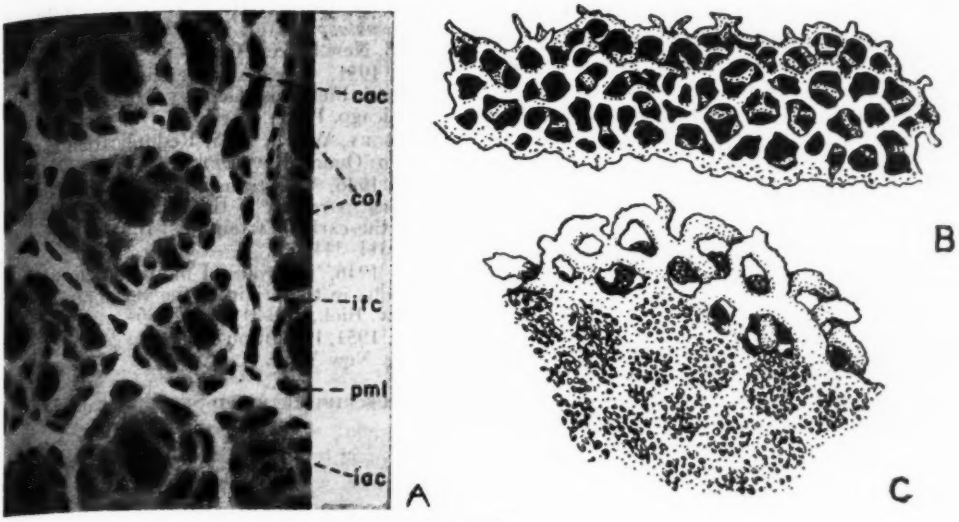


TEXT-FIG. 1—Diagram of external mold of *Paranacystis petrii* Caster.
A. Inferior (plastron) surface. *B*. Superior (carapace) surface. Canal system detail seen on Pl. 74 amplified from the plastron surface at arrow. Modified from Caster (1954).

ing the most superficial level of the plates and adherent to the surrounding shale. In varying degrees the more internal part of the plate-matrix has disappeared. However, a labyrinth of curved, branched and interlacing white strands or rods, firm enough to stand by themselves without support except that provided by the superficial matrix (Text-fig. 2; Pl. 74, fig. 3), projects inward in places where preservation is most complete. The diameter of these rods averages about 0.02 mm., and that of the openings between them (at one time filled with the solid substance of the plate) is from 0.03 to 0.05 mm. No particular pattern can be distinguished in this labyrinth other than an approximate uniformity of size and curvature.

At the points where the white rods connect with the superficial reddish plate-matrix we find that the white material continues into and through that matrix with a pattern like that already described. Consequently on the external pitted and tuberculate surface the white material would be expected to appear as minute dots, like pore-fillings. This is the case, but over some areas it also spreads as a thin superficial film, presumably in the position of the original integument. We infer that the labyrinth is actually a cast of a canal-system penetrating the former matrix of the plates, rather than being a system of structural rods. Substantiating this view is the further detail that at the margins of contiguous plates, whether immovably fixed or not, there appears to be no discontinuity or modification of the labyrinth pattern.

The peduncle of *Paranacystis* consists of a series of about 25 hollow segments of diminishing size, the proximal few of which bear lateral flanges, but in the distal two-thirds of the series a wedge-shaped dorsal crest stands up from each one. The cavity in the lower part continues narrowly up into the crest, between its two side-plates. At the distal margin these plates overlap slightly the next succeeding pair. The canal-system can be found in various degrees of preservation on the inner surfaces of the dorsal plates, the ventral cavities, and in the zone between one such cavity and that next to it. The white material which forms the casts of the canals is, however, unusually abundant here and in some cases forms a dense wall between successive peduncular cavities, in which the canals proper cannot be traced. It may be that this material has replaced a spongy connective tissue in those zones, as well as filling the canals. It is, of course an



TEXT-FIG. 2—Canal details of ostracoderm and carpoid.

A. Sensory canal labyrinth in plates of *Procephalaspis oeselensis* Robertson; internal aspect. ×25 (from Denison, 1951, fig. 374, by permission). *cac*, circumareal sensory canals; *cot*, circumorbital tubercles; *iac*, intra-areal sensory canals; *ifc*, infraorbital lateral line canal; *pml*, processes of middle layer between intra-areal sensory canals.

B. Canals of *Paranacystis petrii* as seen in edge view of marginal plate, ×50.

C. Canals of *P. petrii* in relation to superficial layer of plate; internal aspect, ×100.

open question whether the dimensions of the labyrinth of canals corresponds exactly to the dimensions of the skeletal plates in which it evidently lay, since the matrix of those plates is but slightly shown.

Altogether we find, in proportion to the size of the animal, an impressively large and thick system of skeletal canals. Comparing this with figures of the canal-system in the dermal bones of ostracoderm fishes (Denison, 1951), one is struck by its close resemblance to the sensory canal labyrinth in such types as *Procephalaspis oeselensis* (Text-fig. 2A). Here the canals interlace with one another and form a mesh of connected circles; the only conspicuous difference is that in the fish certain canals are slightly emphasized and make a pattern which can be associated with the lateral line. In the ostracoderms there is also a vascular series of canals lying beneath or internal to the sensory canals, and showing simple or complex structure. The carpoid shows no such internal vascular system. If, then, there is a direct relationship between the two, the carpoid plates are equivalent only to the external layer of the fish plates. But here it is pertinent to notice the relative sizes of these animals. The carpoid is much smaller (maximum length of theca in the type series, 10 mm.), while the fish are at least 2 to 3 inches in length of headshield and do not develop an exoskeleton while smaller. The plates then might be expected to have a thickness adequate for both sets of canals in the fish, while those in the carpoid could not.

One might be tempted at this point to suppose that a good case had been made for interpreting the canals in the carpoid as sensory organs. This is possible, although under the circumstances in which they lived (relatively quiescent on the sea bottom) it is difficult to imagine a need for any such complex system of receptors. But the usual interpretation of pores in the plates of cystoids and carpoids has been that they admitted water for respiration, not into the body cavity but simply into membranous tubes which passed through the plates and permitted osmotic exchange with the body fluids. This is perfectly consistent with the arrangement seen in *Paranacystis*. If a direct relationship between carpoids and ostracoderms, exists, we suggest that these two functions are not mutually exclusive.

It is possible that canals originally functioning in respiration eventually came to possess sensory receptors, and meanwhile surrendered their respiratory function to the more satisfactory pharyngeal gills, along with the development of active swimming and greater size of body. Naturally it would have to be shown that other systems and organs of carpoids and fishes reflect this relationship. This has not yet been done, nor do we argue the point here.

REFERENCES

CASTER, KENNETH E., 1954, A new carpoid echinoderm from the Paraná Devonian: Academia Brasileira de Ciências, Anais, vol. 26, 1954, p. 123–147, 3 pl., 8 fig. Rio de Janeiro, Brazil.

DENISON, ROBERT H., 1947, The exoskeleton of *Trematapsis:* Am. Jour. Sci., vol. 245, p. 337–365. New Haven, Conn.

——, 1951, The exoskeleton of early Osteostraci: Fieldiana: Geology, vol. 11, p. 199–218. Chicago, Ill.

GREGORY, W. K., 1935, Reduplication in evolution: Quart. Rev. Biol., vol. 10, p. 272–290.

——, 1936, The transformation of organic designs: A review of the origin and deployment of the earlier vertebrates: Biol. Rev., vol. 11, p. 311–344.

——, 1946, The roles of motile larvae and fixed adults in the origin of the vertebrates: Quart. Rev. Biol., vol. 21, p. 348–364.

——, 1951, Evolution emerging: 2 vols., Macmillan. New York, N. Y.

MANUSCRIPT RECEIVED SEPTEMBER 12, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 615–645, 16 TEXT-FIG., MAY 1956

THE NORTH AMERICAN ANTHRACOTHERES

J. R. MACDONALD
Museum of Geology, South Dakota School of Mines and Technology

ABSTRACT—The Oligocene and Miocene Anthracotheres of North America are discussed and reviewed. Three Oligocene genera, *Elomeryx*, *Aepinacodon*, and *Heptacodon* are recognized and two genera, *Arretotherium* and *Kukusepasutanka* are recognized from the Miocene. The new genus and species *Kukusepasutanka schultzi* from the early Miocene of Montana is described. A questionable occurrence of the Old World genus *Bothriodon* is recorded from the Oligocene of Nebraska.

INTRODUCTION

THE bunodont artiodactyls of the Oligocene and, to a lesser extent, the Miocene of North America are among the more neglected groups of fossil mammals. The New Word anthracotheres are uncommon elements of these faunas and, in spite of the large collections from these epochs, are not well represented by complete or nearly complete material. They are quite rare in the early Oligocene and early Miocene and reach a quickly lost abundance only in the early Whitneyan Protoceras channels of the Big Badlands. Here, while their actual abundance is greater, their relative abundance is much greater due to the paucity of remains of any kind in these beds.

It is redundant, but perhaps of interest, to repeat the comments of both Troxell and Scott when they remarked on the great confusion in the taxonomy of these forms. Troxell (1921, p. 325) stated in the introduction to his paper on the American Bothriodonts,

> Seldom do we find instances of genera that have been so variously arranged and classified, or a synonomy and precedence that have been more discussed than those of the group of extinct artiodactyls which constitute a part of the Anthracotherinae, including the well known names: *Ancodus* Pomel, *Bothriodon* Aymard, *Elomeryx* Marsh, *Heptacodon* Marsh, *Hyopotamus* Owen, and *Octacodon* Marsh. In the present it has been necessary to use our own American generic names, adding one new one, in order to bring out the distinctions, from the European forms, which exist in every known case; but one cannot resist the impulse to attempt to settle Old World difficulties and matters of synonymy are no exception.

Scott (1940, p. 443) while erecting the subfamily "Bothriodontinae" states,

> As fossils of this subfamily are not common in the White River beds, comparatively few paleontologists have dealt with them. Nevertheless, a great confusion of synonymy has arisen among them, largely because of unsuccessful attempts to apply the European nomenclature to American fossils and that nomenclature itself has been much confused and overloaded with synonyms.

The following report is an attempt to bring the story of the North American anthracotheres up to date by the description of material which was not available at the time that Scott reviewed the White River Oligocene mammalian faunas and by the inclusion of a new record of *Heptacodon* from the Yoder member of the Chadron formation of Wyoming, which represents the oldest record of an anthracothere in North America, by the description of a new form from the early Miocene of Montana, and the recording of various isolated specimens. Most of the new material is in the collections of the Museum of Geology at the South Dakota School of Mines and Technology. This material from the Big Badlands was collected from the Protoceras channels during the past 25 years by James D. Bump and his associates in the Museum of Geology. Much of this material was discovered in 1940 during a field season which was supported by the National Geographic Society (Connolly & Bump, 1946). The few available specimens from the Miocene are also discussed. One of these, the type of *Arretotherium fricki* Macdonald & Schultz (1956), was made available through the courtesy of C. Bertrand Schultz of the University of Nebraska State Museum; and the other *Kukusepasutanka schultzi*, n. sp., which is described below, was kindly lent to the writer by Childs Frick.

As there has been no additional skeletal material made available since Scott's White River monograph was published, a discus-

sion of the general osteology of the anthracotheres has not been included in this paper as it is felt that Scott (1894, 1940) has adequately covered the subject. As a point of interest it should be recorded that late in August 1954 the nearly complete skeleton of a juvenile *Heptacodon* was collected by John Clark for the Princeton University Museum. This skeleton was found at the top of the Chadron at Saddlehorse Pass in the Big Badlands. At this time it has not been prepared and is therefore unavailable for description.

ACKNOWLEDGMENTS

My thanks are due to Childs Frick of the Frick Laboratories, C. L. Gazin and D. H. Dunkle of the Smithsonian Institution, J. T. Gregory of the Peabody Museum, C. W. Hibbard of the Museum of Paleontology of the University of Michigan, G. L. Jepsen of the Princeton University Museum, LeRoy Kay of the Carnegie Museum, Bryan Patterson of the Chicago Natural History Museum, M. M. Payne of the National Geographic Society, H. G. Roberts of the Academy of Natural Sciences of Philadelphia. A. S. Romer of the Museum of Comparative Zoology, G. G. Simpson of the American Museum of Natural History, C. B. Schultz of the University of Nebraska State Museum, and R. W. Wilson of the University of Kansas Natural History Museum for allowing me to use and study specimens in their respective museums.

The drawings were made by Orla Peters and Charlotte Snyder.

Funds for carrying out this study were made available by the National Science Foundation in Grant No. NSF-G254.

HISTORICAL SUMMARY OF THE STUDY OF THE NORTH AMERICAN ANTHRACOTHERES

As in the case with many of the Middle Tertiary forms from the continental sediments of western North America, the anthracotheres were first dealt with by Joseph Leidy. He described *Hyopotamus americanus* in 1856 and figured the type in his monograph of 1869. This species was represented by two maxillary fragments with the molars and posterior premolars and an isolated lower cheek tooth. O. C. Marsh, who described most of the New World forms established *Hyopotamus deflectus* in 1890. His description was based on a skull. This species was not figured until many years later, when Troxell (1921) published the first review of the American Bothriodonts. The highwater mark for studies of this group was reached in 1894 when eight species were described by Marsh, Osborn & Wortman, and Scott. In addition, Scott published an osteology of *Ancodus* [*Elomeryx brachyrhynchus*] based on a skeleton collected from the Protoceras channels by Hatcher for the Princeton Museum. The following years were marked by desultory work on this group with Douglass describing the first form from the American Miocene in 1901 when he published the name *Arretotherium acridens* Douglass based on some fragments from the early Miocene of Montana. Lambe described *Anthracotherium pygmaeum* from the early Oligocene of the Cypress Hills of Canada in 1908 and Matthew described *Ancodus leptodus* from South Dakota. Both of these species may be considered as nomina vana, as the former is based on a tooth fragment that is probably referable to *Heptacodon* and the latter is based on such a poor specimen that little can be interpreted from it.

The first partial review of the group was made by Troxell (1921) when he discussed the forms represented in the Marsh collections at the Yale University Museum. At that time he erected the genus *Aepinacodon* to hold the Oligocene species not referable to *Heptacodon*, *Octacodon*, and *Elomeryx*. In 1940, Scott's Artiodactyla section of the White River monograph was published and in this volume he partially reviewed the group and presented a comprehensive review of the osteology of the forms with known post-cranial skeletal parts. This review, of course, did not include the Miocene genus *Arretotherium* and, possibly through inadvertence, some of the lesser known Oligocene forms. It is interesting to note that E. D. Cope did no work on Anthracotheres and only mentioned the group a few times in general papers on broad phases of paleontology.

THE BOTHRIODONTINAE SCOTT

Scott (1940, p. 443) proposed the subfamily Bothriodontinae for those anthracotheres with cusps of the upper molars distinctly crescentic and the canines not de-

veloped into tusks. This name was coined to replace Gill's name "Hyopotaminae" which became untenable when *Hyopotamus* Owen was shown to be a synonym of *Bothriodon* Aymard.

In order properly to use subfamily designations within this family a complete review of all the anthracotheres should be made. It is quite probable that *Heptacodon* and *Kukusepasutanka* should not be included in the same subfamily as the other New World genera; and there certainly is no point in establishing two more subfamilies until the entire group has been reviewed as a unit and relationships between all of the genera established. It is therefore suggested that this name not be used and that no formal subfamily designations be applied to the North American forms until such a time as all of the two dozen described genera can be reviewed and evaluated.

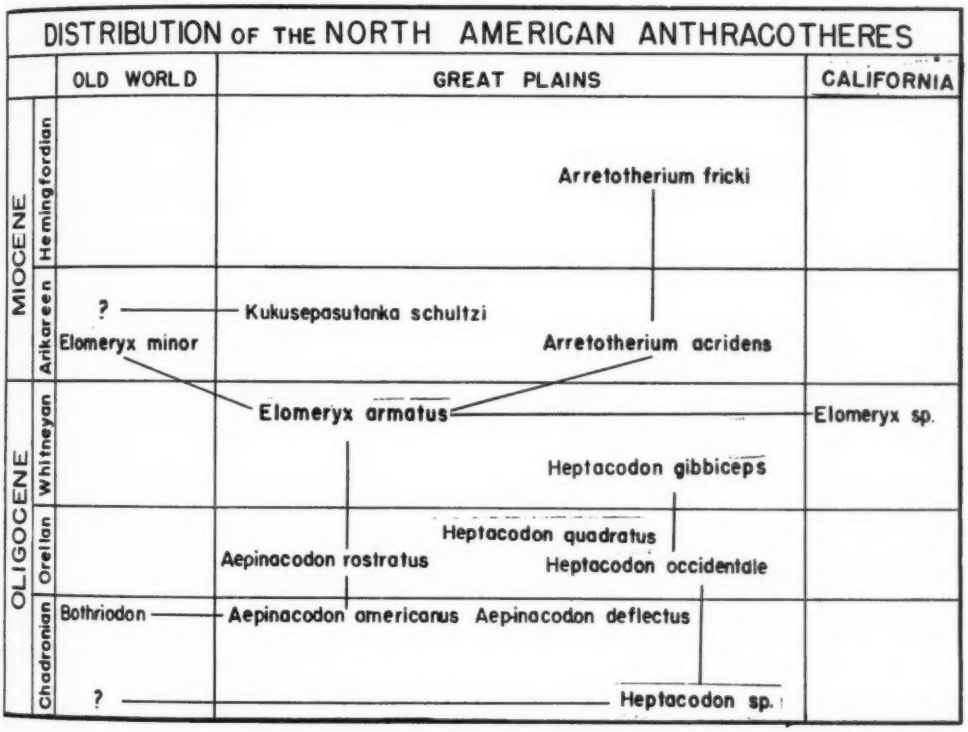
SYSTEMATIC PALEONTOLOGY
THE GENERA OF NORTH AMERICAN ANTHRACOTHERES

A review of the available anthracothere material in the nation's museums reveals that five genera of anthracotheres may be recognized in the Oligocene and Miocene deposits of North America. These genera include *Aepinacodon* Troxell (1921), *Elomeryx* Marsh (1894) *Heptacodon* Marsh (1894), *Arretotherium* Douglass (1901), and *Kukusepasutanka*, n. gen. A pair of toothless mandibles from the Oligocene of Nebraska may be the only New World record of *Bothriodon*. These genera may be distinguished by the characteristics indicated on the accompanying chart (Table 1).

Genus AEPINACODON Troxell

Aepinacodon Troxell. TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 334.
Hyopotamus Leidy (*nec* Owen). LEIDY, 1856, Acad. Nat. Sci. Philadelphia, Proc., vol. 8, p. 59.
Hyopotamus Marsh (*nec* Owen). MARSH, 1890, Am. Jour. Sci., vol. 37, p. 524.
Ancodus Scott (*nec* Owen). SCOTT, 1894, Jour. Acad. Nat. Sci. Philadelphia, vol. 9, p. 461.
Bothriodon Scott (*nec* Aymard). SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 458.

Type species.—*Hyopotamus deflectus* Marsh.



TEXT-FIG. 1

TABLE 1.—KEY TO THE GENERA OF NORTH AMERICAN ANTHRACOTHERES

	Aepinacodon	*Elomeryx*	*Heptacodon*	*Arretotherium*	*Kukusepasutanka*
Incisors	Simple	Simple	Simple	Simple	Unknown
Canine	Incisiform	Incisiform or canineiform	Tusk-like	Laterally compressed	Unknown
P^1	Laterally compressed or missing	Laterally compressed or missing	Laterally compressed	Strongly laterally compressed	Unknown or missing
P^2	Laterally compressed	With lingual-posterior heel, compressed diagonal blade	Moderately laterally compressed	Strongly laterally compresed or as in *Elomeryx*	With lingual-posterior heel, compressed diagonal blade
P^3	With lingual-posterior heel, compressed diagonal blade	Similar to P^2	Single cusp, triangular base	Single cusp with triangular base or as in *Elomeryx*	Similar to P^4
P^4	Bicuspid	Bicuspid	Bicuspid	Bicuspid, paracone deeply notched labially	Bicuspid, paracone deeply notched labially
M^{1-3}	Mesostyle invaded by transverse valley		Prominent parastyle, mesostyle not invaded by transverse valley	No protoconule, mesostyle invaded by transverse valley, deeply notched	Mesostyle invaded by transverse valley, para-, meso-, and metastyles prominent and bulbous
General	Internal nares opens just behind or between M^3's	Internal nares opens well behind the M^3's	Short diastema between P^1 and canine	No diastema between P^1 and canine	Tubular snout, massive teeth, bulbous stylar cusps

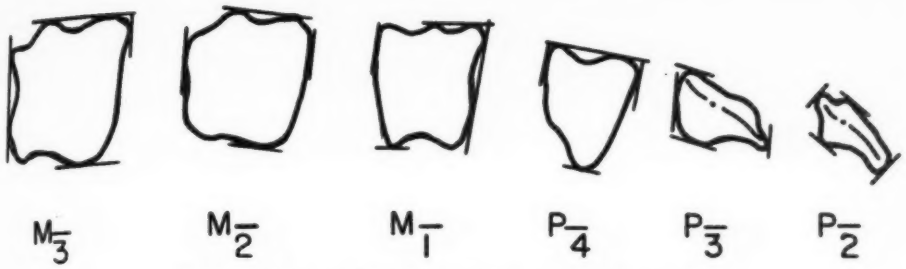
Range.—Early to middle Oligocene, North America.

Diagnosis.—Upper molars with transverse groove, particularly in M^3, with tendency to curve posteriorly between protocone and hypocone; hypocone relatively smaller than *Elomeryx*, mesostyle and parastyle less bulbous, muzzles shorter, and canines less prominent than in *Bothriodon*.

Discussion.—Troxell (1921, p. 334) proposed the name *Aepinacodon*, for the North American Oligocene anthracotheres that were not referable to *Elomeryx*, *Octacodon*, or *Heptacodon*. In particular he included *Hyopotamus americanus* Leidy, *H. deflectus* Marsh, and *Ancodon rostratus* Scott. Scott rejected this name in his White River monograph and referred the species *A. americanus* and *A. rostratus* to the European genus *Bothriodon* and ignored Marsh's species *H. deflectus*. Although Scott does not actually say so one gets the impression that he considered the New World forms to represent a "species group" or even a subgenus which he defined but did not name. Actually it appears that there is enough difference between the European species of *Bothriodon* and the American species which have been assigned to that genus to revive Troxell's name *Aepinacodon* and refer these species to it.

Troxell (1921, p. 336) distinguished *Aepinacodon* from *Hyopotamus* as typified by *H. bovinus* Owen, on the basis of the following characteristics:

[*1*] —by the curved transverse groove and
[*2*] the resulting decrease in size of the Hypocone,
[*3*] by the closer grouping of the cusps transversely,
[*4*] by the narrower mesostyle,
[*5*] and by the greater relative length of the molars antero-posteriorly.



TEXT-FIG. 2—Method of measuring upper cheek teeth.

and from *Bothriodon* Aymard, of which *Hyopotamus* is now considered a synonym by:

[1] —the unreduced premolars,
[2] and absence of diastema behind P2/,
[3] the curved transverse valleys of the molars,
[4] their narrower outer borders,
[5] the grouped cusps,
[6] the rougher character with an abundance of tubercles and cingula,
[7] the less elongated muzzle,
[8] the less forward position of the posterior nares,
[9] the more completely enclosed orbit,
[10] and the narrow supra-occipital of *Aepinacodon*.

Scott (1940, p. 458) concluded that these characteristics were not enough to separate the American species from the European forms but he did distinguish between them as follows:

> The diagnostic features of the American *Bothriodon* are: (1) the small canines, which are not at all tusk-like; (2) diastemata between canines and molars; (3) very elongate rostrum; (4) forward position of posterior nares, which open between the molar teeth. The peculiar molar pattern is common to *Elomeryx*.

I believe that the American forms are sufficiently distinct to be grouped together into a separate genus and that *Aepinacodon* Troxell should be resurrected. Although there is a variation within these species which was not known to Troxell when he defined the genus, many of his generic characters are still valid.

Three species may be referred to this genus: *A. americanus* (Leidy) and *A. deflectus* (Marsh) from the early Oligocene Chadronian and *A. rostratus* (Scott) from the middle Oligocene Orellan. The determination of species among anthracotheres presents the same problems that one encounters among so many Early and Middle Tertiary forms. There is so much variation within the group that one could easily assign a different specific name to almost each specimen.

In general the last two upper molars are the only part of the animal that can be practically used in specific identification. Usually the M^1 is badly worn by the time that the last two molars are fully erupted or, if the M^1 is unworn, the last molar is either unerupted or not formed within the maxillary. The premolars do not seem to be of great significance in specific determination and the anterior portion of the rostrum is quite often missing. The very low incidence of association of lower jaws with craniums makes identification of species by lower dentitions virtually impossible. Scott has used the presence or absence of the P^1 as a specific characteristic of *A. rostratus* and *A. americanus* but, in any form which is undergoing tooth reduction, this difference is not always reliable.

Among the crania of *Elomeryx armatus* Marsh from the Protoceras channels in the Poleslide member of the Brule formation one is without P^1's and one other has the P^1 on one side only.

AEPINACODON AMERICANUS (Leidy)

Hyopotamus americanus Leidy, LEIDY, 1856a, Acad. Nat. Sci. Philadelphia, Proc., vol. 8, p. 59. LEIDY, 1856b, Am. Jour. Sci., vol. 21, p. 422–423.

Choeropotamus (*Hyopotamus*) *americanus* (Leidy). LEIDY, 1857, Acad. Nat. Sci. Philadelphia, Proc., vol. 9, p. 89. HAYDEN, 1858, idem, vol. 10, p. 157.

Hyopotamus americanus LEIDY, 1869, Acad. Nat. Sci. Philadelphia, Jour., vol. 7, p. 202, 389, pl. xxi, fig. 1–6. LEIDY, 1871, U. S. Geol. Survey of Wyoming and portions of contiguous Territories, 2d (4th) annual report, F. V. Hayden, U. S. Geologist, p. 355. KING, 1878, Systematic geology: U. S. Geol. Explor. 40th parallel, Clarence King, geologist in

charge, vol. 1, p. 411. OSBORN & WORTMAN, 1894, Am. Mus. Nat. Hist. Bull., vol. 6, p. 219, fig. 6a.

Ancodus (*Hyopotamus*) *americanus* (Leidy). SCOTT, 1894, Acad. Nat. Sci. Philadelphia, Jour., vol. 9, p. 461, pl. 23, fig. 2–3.

Hyopotamus americanus Leidy. MATTHEW, 1899. Am. Mus. Nat. Hist. Bull., vol. 12, p. 59. MATTHEW, 1901, Am. Mus. Nat. Hist., Mem., 1, p. 369.

Ancodon americanus (Leidy). HAY, 1902, U. S. Geol. Surv. Bull. 179, p. 652. MATTHEW, 1909. Am. Mus. Nat. Hist. Bull., vol. 26, p. 1, 3, 5, 6.

Hyopotamus americanus Leidy. OSBORN, 1909, U. S. Geol. Surv. Bull. 161, p. 127. O'HARRA, 1910, South Dakota Sch. Mines, Bull., vol. 9, p. 107

Ancodon americanus (Leidy). COOK, 1912, Nebraska Geol. Survey, vol. 7, p. 35.

Hyopotamus americanus (Leidy). DEPERET, 1912, Internat. Zool. Congr. Proc., vol. VII, Boston, 1907, p. 708. O'HARRA, 1920, South Dakota Sch. Mines Bull., vol. 13, p. 150.

Aepinacodon americanus (Leidy). TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 334. HAY, 1930. Carnegie Inst. Washington, Pub. 390, p. 760. CLARK 1937, Ann. Carnegie Mus., vol. 25, p. 322.

Bothriodon americanus (Leidy). SCOTT, 1940, Am. Philos. Soc. Trans., vol. 28, p. 463–464, pl. 45.

Type.—Two maxillary fragments with the left M^{1-3} and right P^{3-4}, and a lower molar. ANSP 10581, 10582, 10583 and 10584. This probably is a mixed type. Consequently, the upper molars, 10583 and 10584 should be considered the type.

Type locality.—"the Mauvaises Terres of White River."

Horizon.—Peanut Peak member, Chadron formation.

Age.—Chadronian.

Type figure.—Leidy, 1869, pl. xxi, fig. 1–6.

Diagnosis.—M^{2-3} with posterior cingulum from linguad of crest of hypocone to base of metastyle; mesostyle broad, curves lingually over end of transverse valley which has pointed lingual end; enamel heavily crenulated. P^4 compressed antero-posteriorly on labial side, no lingual cingulum.

Discussion.—Scott (1940, p. 463) referred two skulls to this species. The first, a very fine cranium (PU 13691) with unworn dentition, is in the Princeton University Museum. The other, a cranium (UM 18210) of a very old individual with many missing teeth and the remainder badly worn, is in the Museum of Paleontology at the University of Michigan. There is an additional partial cranium (USNM 4134) in the United States National Museum, which shows the characteristics enumerated above. Each of these specimens was collected in the Big Badlands of South Dakota and the first two are from the Chadron formation. The later specimen was collected by Hatcher in 1890. The horizon is not indicated but presumably it is also from the Chadron.

Scott (1940, p. 464) gives the following additional characteristics for this species. "The present species differs from *B. rostratus* in the constant presence of the first upper premolar, P^1. The second and third premolars, P^2 and P^3, are implanted obliquely to the median line. In the upper molars the external crescents are carried over far toward the lingual side, narrowing the longitudinal valley. The occiput is comparatively high dorsally, descending obliquely outward on the sides. The two broad and rounded ridges which diverge from the foramen magnum to the occipital crest are prominent and the lateral fossae external to them are deep. In the Michigan skull the pterygoids end ventrally in conspicuous, elongate and slender hamular processes; that the other skulls lack. These are probably one of the accidents of collecting."

These characteristics seem to be essentially correct although the oblique orientation of P^{2-3} possibly is open to interpretation as it is a function of the "pinching in" of the rostrum. A similar situation is seen in the Pliocene hyaenoid dog, *Osteoborus diabloensis* Richey, where there is a great deal of variation in the spacing and orientation of the individual premolars in various specimens from the same quarry. (Macdonald, 1949, fig. 5, 7). The narrowing of the transverse valley is not a conspicuous feature and also would be an intangible characteristic that would not appear the same to two different observers.

In light of the type of material that is usually recovered, more dependence in identification should be placed on the more obvious dental characteristics.

AEPINACODON DEFLECTUS (Marsh)

Hyopotamus deflectus Marsh. MARSH, 1890. Am. Jour. Sci., vol. 37, p. 524.

Ancodon deflectus (Marsh). MARSH, 1894, Am. Jour. Sci., vol. 48, p. 178, fig. 7. SCOTT, 1894, Acad. Nat. Sci. Philadelphia, Jour., vol. 9, p. 461.

Table of Measurements (mm.)[1]

	Type	P.U. 13691	USNM 4134		UM 18210	
		Right	Right	Left	Right	Left
P^1 A-P diam.					8.6	
P^1 Tr diam.					4.4	
P^2 A-P diam.		16.2			17.3	
P^2 Tr diam.		8.8			9.6	
P^3 A-P diam.	21.5	20.8		19.9	21.3	
P^3 Tr diam.	15.2	17.1		15.6	16.5	
P^4 A-P diam.	12.5	14.5			15.2	
P^4 Tr diam.	19.2	20.5			19.8	
M^1 A-P diam.	20.5	21.2				
M^1 Tr diam.	28.9	24.2				
M^2 A-P diam.	27.0	29.1				
M^2 Tr diam.	28.8	29.1				
M^3 A-P diam.	28.7	31.9	31.9	27.2		30.0
M^3 Tr diam.	30.8	33.2	31.5	30.2		31.7
P^2–M^3		128.0				
P^3–M^3		113.0	98.9	95.5		
P^4–M^3		96.8				
M^{1-3}		81.5				

[1] See Text-fig. 2 for method used by the author in measuring teeth.

Hypotamus deflectus Marsh. MATTHEW, 1899, Am. Mus. Nat. Hist. Bull., vol. 12, p. 59.
Ancodon americanus (Marsh). HAY, 1902, U. S. Geol. Survey Bull. 179, p. 653.
Aepinacodon deflectus (Marsh). TROXELL, 1921. Am. Jour. Sci., vol. 1, p. 337, fig. 7. HAY, 1930, Carnegie Inst. Washington, Pub. 390, p. 730.

Type.—Partial skull. YPM 11802.

Type locality.—Big Badlands, South Dakota.

Horizon.—Peanut Peak member, Chadron formation.

Age.—Chadronian.

Type figure.—Troxell, 1921, fig. 6,7.

Diagnosis.—M^3 with transverse valley ending in square notch in mesostyle; posterior cingulum broken into nodules between hypocone and metastyle, connects to neither, small spur on hypocone represents lingual cingulum; hypocone and protocone meet in transverse valley. M^2 with transverse valley blocked by hypocone and protocone; lingual cingulum between hypocone and protocone. P^4 without lingual cingulum; broad anterior and posterior cingulum, protocone isolated and pillar-like. Lower molars with cingula broken into a series of small tubercles.

Discussion.—This species presents a special problem as the primary specific characteristics are not found on both the right and left dentition. Troxell's (1921, p. 337) reappraisal of the species is based on the right upper dentition. As a result of this difference the species has been either ignored or referred to *A. americanus*. It seems reasonable at this time to recognize this species in spite of this situation as the form of the P^4 and the position of the cingulum on the M^{2-3} is quite different from any of the specimens that may be referred to *A. americanus*. The lower jaw is quite distinctive in that the cingula of the lower teeth are broken into a great number of small tubercles. While it is realized that this may represent a minor mutation found only in this individual, it must be accepted at face value until such a time as enough material is available to determine its real significance. This condition is not found in the lower jaw (PU 11172) which was associated with the Princeton University skull of *A. rostratus*. These are the only recorded associated jaws of *Aepinacodon*.

Table of measurements (mm.)

P^3 A-P diam.	21.5
P^3 Tr diam.	17.3
P^4 A-P diam.	15.8
P^4 Tr diam.	20.4
M^1 A-P diam.	20.2
M^1 Tr diam.	23.3
M^2 A-P diam.	26.4
M^2 Tr diam.	27.1
M^3 A-P diam.	26.8
M^3 Tr diam.	30.8
P^2–M^3	102.3
P^4–M^3	85.8
M^{1-3}	53.3

AEPINACODON ROSTRATUS (Scott)

Ancodus rostratus Scott. SCOTT, 1894, Acad. Nat. Sci. Philadelphia, Jour., vol. 9, appendix, p. 536.

Ancodon rostratus (Scott). HAY, 1902, U. S. Geol. Survey Bull. 179, p. 653.
Bothriodon rostratus (Scott). TROUESSART, 1905, Catalogus Mammalium tam viventium quam fossilium, p. 651.
Ancodon rostratus (Scott). MATTHEW, 1909, Am. Mus. Nat. Hist., Bull., vol. 26, p. 1, 3, 5.
Hyopotamus rostratus (Scott). MATTHEW, 1909, U. S. Geol. Survey Bull. 361, p. 106.
Ancodon rostratus (Scott). COOK, 1912, Nebraska Geol. Survey, vol. 7, p. 37.
Hyopotamus rostratus (Scott). O'HARRA, 1920, South Dakota Sch. Mines, Bull., vol. 13, p. 152.
Aepinacodon rostratus (Scott) TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 377.
Bothriodon rostratus (Scott). SCOTT, 1937, A history of the land mammals of the Western Hemisphere, p. 385. SCOTT, 1940. Am. Phil. Soc., Trans., vol. 28, p. 464–466, pl. 46.

Type.—A skull, PU 11172.

Type locality.—Big Badlands, South Dakota.

Horizon.—Metamynodon channels, of Scenic member, Brule formation.

Age.—Orellan.

Type figure.—Scott, 1940, pl. XLVI.

Diagnosis.—M^3 with wide open transverse valley; mesostyle deeply notched; hypocone larger than in other species. M^2 similar to M^3 but mesostyle not notched. P^4 with heavy cingulum continuous around protocone.

Discussion.—Scott (1940, p. 465) emended and expanded his original description of this species as follows:

(1) P^1 has been lost, making the premolar formula $\frac{3}{3}$ quite consistently;
(2) P^2 and P^3 are not inserted obliquely to the median line;
(3) the external crescents of the upper molars are not, as it were pushed so far toward the lingual side, so that the longitudinal valley is wider;
(4) the occiput is of different shape, being lower dorso-ventrally and the crest describing an almost regular halfcircle, and the two ridges which diverge from the foramen magnum to the crest are much less prominent;
(5) the paroccipitals are decidedly longer and the post-tympanic processes of the squamosals are much more prominent;
(6) the temporal openings are relatively longer antero-posteriorly.

This species is well enough characterized by the shape of the transverse valley and the heavy cingulum of P^4 to be readily distinguished from the other two known Oligocene species. The presence or absence of P^1 may or may not be a significant feature as forms which are in the process of tooth reduction may vary from individual to individual or on the two sides of the jaw of the same individual.

The lower dentition of this genus is known in association with crania from this species and *Aepinacodon deflectus* (Marsh). The incisors are broad based and broadly rounded on the anterior and posterior blades with a narrow slightly recurved apex formed by the junction of three ridges; the anterior and posterior blades, which are bent lingually, and a median lingual ridge that arises from the base of the crown just posterior to the center of the tooth. The

Table of measurements (mm.)

	Right	Left
Lower dentition		
Canine A-P diam.	14.5	
Canine Tr diam.	11.0	
Diastema C-P_1		19.6
Alveolus P_1 A-P diam.		10.2
Alveolus P_1 Tr diam.		5.5
Diastema P_{1-2}		52.1
P_2 A-P diam.	8.1	8.5
P_2 Tr diam.	6.6	7.1
Diastema P_{2-3}	1.2	5.9
P_3 A-P diam.	17.3	17.7
P_3 Tr diam.	10.8	11.1
P_4 A-P diam.	20.6	20.1
P_4 Tr diam.	13.3	
M_1 A-P diam.	17.8	16.5
M_1 Tr diam.		?14.8
M_2 A-P diam.	21.4	24.2
M_2 Tr diam.	16.5	17.1
M_3 A-P diam.	39.1	38.9
M_3 Tr diam.	18.8	18.8
P_2–M_3	138.7	134.5
M_{1-3}	80.7	82.6
Upper Dentition		
I^2 A-P diam.	14.2	14.3
I^2 Tr diam.	10.3	9.7
Diastema I^{2-3}	4.7	5.8
I^3 A-P diam.	12.3	13.0
I^3 Tr diam	9.1	8.7
Diastema I^2—Canine	10.8	8.5
Canine A-P diam.		15.6
Canine Tr diam.	9.8	9.8
Diastema Canine—P^2	90.5	89.8
P^2 A-P diam.	16.5	16.3
P^2 Tr diam.	10.8	11.8
P^3 A-P diam.	20.8	20.7
P^3 Tr diam.	17.2	19.5
P^4 A-P diam.	14.6	15.6
P^4 Tr diam.	19.3	18.8
M^1 A-P diam.	?19.2	20.4
M^1 Tr diam.		21.9
M^2 A-P diam.	24.9	25.4
M^2 Tr diam.	27.3	27.5
M^3 A-P diam.	28.5	28.5
M^3 Tr diam.	30.1	31.0
P^2–M^3	119.8	120.0

labial surface is broadly rounded and the lingual surface has two prominent sulci between the ridges. The canine is separated from the I_3 by a long diastema, the alveoli indicate that it is smaller than the incisors. The premolars are basically similar to the incisors, with lingually directed anterior and posterior blade ridges and a median lingual ridge. The cingula are discontinuously developed on the various teeth which become increasingly complex from anterior to posterior. The molars are bunoselenodont with conical metaconids and entoconids and crescentic protoconids and hypoconids. Cingula are discontinuous and confined to the anterior, posterior and labial sides. The M_3 has a well developed talonid with a single posterior cusp and two strong ridges which run antero-lingually to join the trigonid at the base of the entoconid.

AEPINACODON sp.

Ancodus (Hyopotamus) brachyrhynchus Osborn & Wortman. LAMBE, 1908, Contrib. Canadian Paleont., vol. 3, pt. iv, p. 24, pl. II, fig. 1–9.
Bothriodon brachyrhynchus (Osborn & Wortman). RUSSELL, 1934, Royal Canadian Inst. Trans., vol. 20, pt. 1, p. 53.

A collection of miscellaneous isolated teeth from the Cypress Hills of Saskatchewan were described and figured by Lambe (1908, p. 24) and referred to *Ancodus brachyrhynchus* in spite of the fact that most of the Cypress Hills material was Chadronian in age. Russell (1934, p. 53) listed his material as *Bothriodon brachyrhynchus* (Osborn & Wortman) but the material is probably not specifically determinate.

AEPINACODON sp.

Anthracotheriid sp. GALBREATH, 1953, Univ. Kansas Paleont. Contr., art. 4, p. 86.

A tooth fragment that is probably referable to *Aepinacodon* was reported by Galbreath from the Cedar Creek member of the White River Formation in northeastern Colorado.

Genus ELOMERYX Marsh

Elomeryx Marsh. MARSH, 1894c, Am. Jour. Sci., vol. 48, p. 176.
Heptacodon Marsh (in part). MARSH, 1894b, Am. Jour. Sci., vol. 48, p. 93.
Hyopotamus Osborn & Wortman (*nec* Owen). OSBORN & WORTMAN, 1894, Am. Mus. Nat. Hist., Bull., vol. 6, p. 220.

Type species.—*Heptacodon armatus* Marsh.

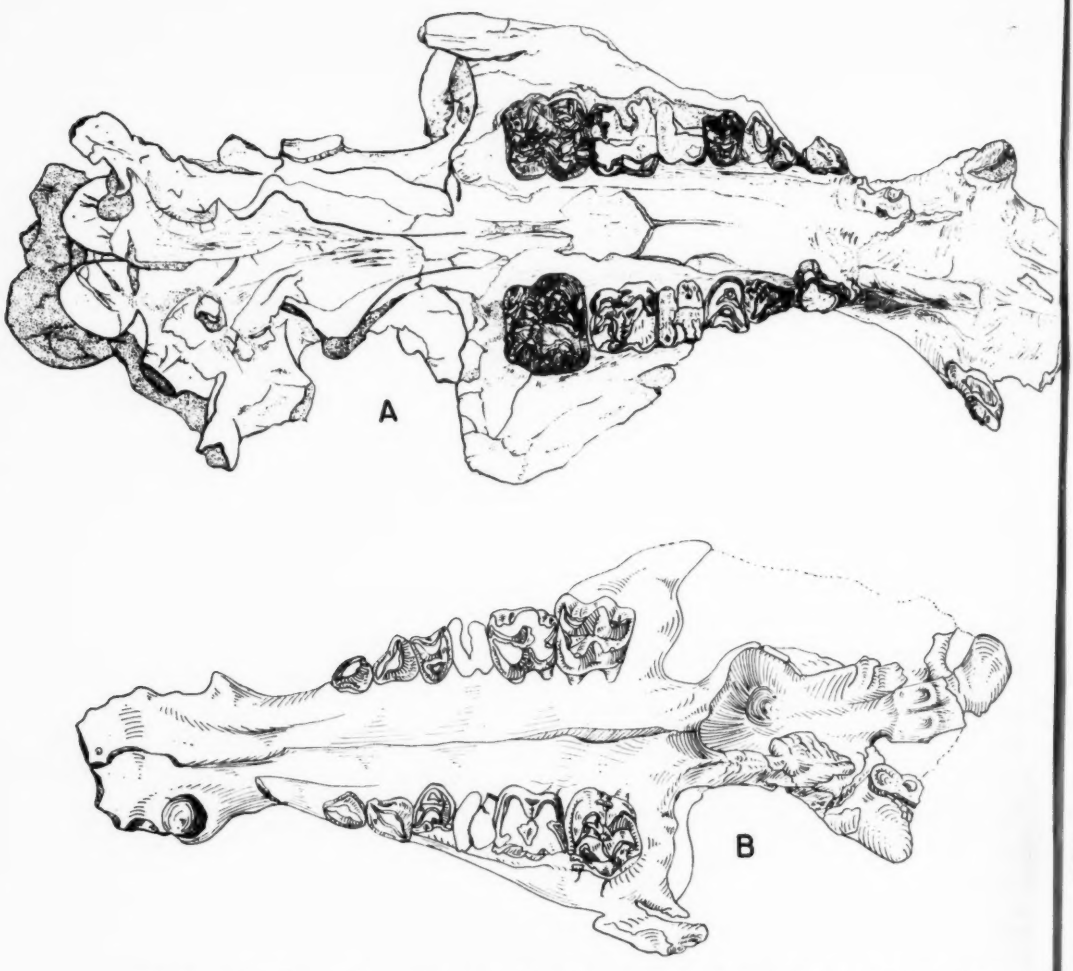
Range.—Late Oligocene, North America; Early Miocene, Europe.

Diagnosis.—Upper cheek teeth as in *Aepinacodon*; M^{1-3} with prominent transverse groove entering mesostyle; posterior cingulum strongly connected to metastyle; rostrum shorter than in *Aepinacodon* without long diastema between canine and P^1; palatines extend posteriorly to form long tubular prolongation of nasal canal.

Discussion.—*Elomeryx* March (1894) is easily distinguished from *Aepinacodon* by the posterior elongation of the palate into a tubular nasal canal. Although the dentition of these genera are quite similar, there are minor consistent differences. Again, due to the low incidence of association of upper and lower dentitions, the characteristics of the upper teeth are of the greater importance.

ELOMERYX ARMATUS (Marsh)
Text-fig. 3–7

Heptacodon armatus Marsh. MARSH, 1894b, Am. Jour. Sci., vol. 48, p. 93, fig. 2.
Elomeryx armatus (Marsh). MARSH, 1894c, Am. Jour. Sci., vol. 48, p. 176, fig. 3,4.
Anthracotherium karense Osborn & Wortman. MATTHEW, 1899, Am. Mus. Nat. Hist., Bull., vol. 12, p. 59.
Elomeryx armatus (Marsh). HAY, 1902, U. S. Geol Survey Bull. 179, p. 652.
Species indeterminate. MATTHEW, 1909, Am. Mus. Nat. Hist., Bull., vol. 26, p. 6.
Elomeryx armatus (Marsh). TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 331, fig. 4. HAY, 1930, Carnegie Inst. Washington, Pub. 390, p. 759. SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 471–472. SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 472.
Elomeryx mitis Marsh. MARSH, 1894c, Am. Jour. Sci., vol. 48, p. 176, fig. 5.
Anthracotherium mitis (Marsh). MATTHEW, 1899, Am. Mus. Nat. Hist., Bull., vol. 12, p. 59.
Elomeryx mitis March. HAY, 1902, U. S. Geol. Survey, Bull. 179, p. 652.
Species indeterminate. MATTHEW, 1909, Am. Mus. Nat. Hist., Bull., vol. 26, p. 7.
Elomeryx armatus (Marsh). TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 334.
Elomeryx mitis Marsh. HAY, 1930, Carnegie Inst. Washington, Pub. 390, p. 759.
Elomeryx armatus (Marsh). SCOTT, 1940. Am. Philos. Soc., Trans., vol. 28, p. 471.
Hyopotamus brachyrynchus Osborn & Wortman. OSBORN & WORTMAN, 1894, Am. Mus. Nat. Hist., Bull., vol. 6, p. 220, fig. 6b.
Ancodus brachyrynchus (Osborn & Wortman). SCOTT, 1894, Geol. Mag., 1, p. 492. SCOTT, 1894, Acad. Nat. Sci. Philadelphia, Jour., vol. 9, pl. 23, fig. 1, pl. 24, fig. 5–8.



TEXT-FIG. 3—*Elomeryx armatus*, two palates showing sexual variation in the shape of the rostrum: *A*, male, SDSM 2821; *B*, female, SDSM 4061, ×½.

Hyopotamus brachyrynchus (Osborn & Wortman). WOODWARD, 1898, Outlines of vertebrate paleontology for students of zoology, p. 350, fig. 200. MATTHEW, 1899, Am. Mus. Nat. Hist., Bull., vol. 12, p. 59.

Ancodon brachyrynchus (Osborn & Wortman). MATTHEW, 1901, Am. Mus. Nat. Hist., Mem. 1, p. 370. HAY, 1902, U. S. Geol. Survey, Bull. 179, p. 653. MATTHEW, 1909, Am. Mus. Nat. Hist., Bull., vol. 26, p. 1, 3, 5.

Hyopotamus brachyrynchus (Osborn & Wortman). MATTHEW, 1909, U. S. Geol. Survey, Bull. 361, p. 109. O'HARRA, 1910, South Dakota Sch. Mines, Bull., vol. 9, p. 107, fig. 15.

Ancodus brachyrynchus (Osborn & Wortman). GREGORY, 1910, Am. Mus. Nat. Hist., Bull., vol. 27, p. 405, fig. 26. COOK, 1912, Nebraska Geol. Survey, vol. 7, p. 39.

Hyopotamus brachyrynchus (Osborn & Wortman). DEPERET, 1912, Internat. Zool. Cong., Proc., vol. 7, Boston, 1907, p. 708. SCOTT, 1913, A history of the land mammals in the western hemisphere, p. 371, fig. 196.

Brachyodus brachyrynchus (Osborn & Wortman). ABEL, 1914, Die vorzeitlichen Säugetiere, p. 164, fig. 116.

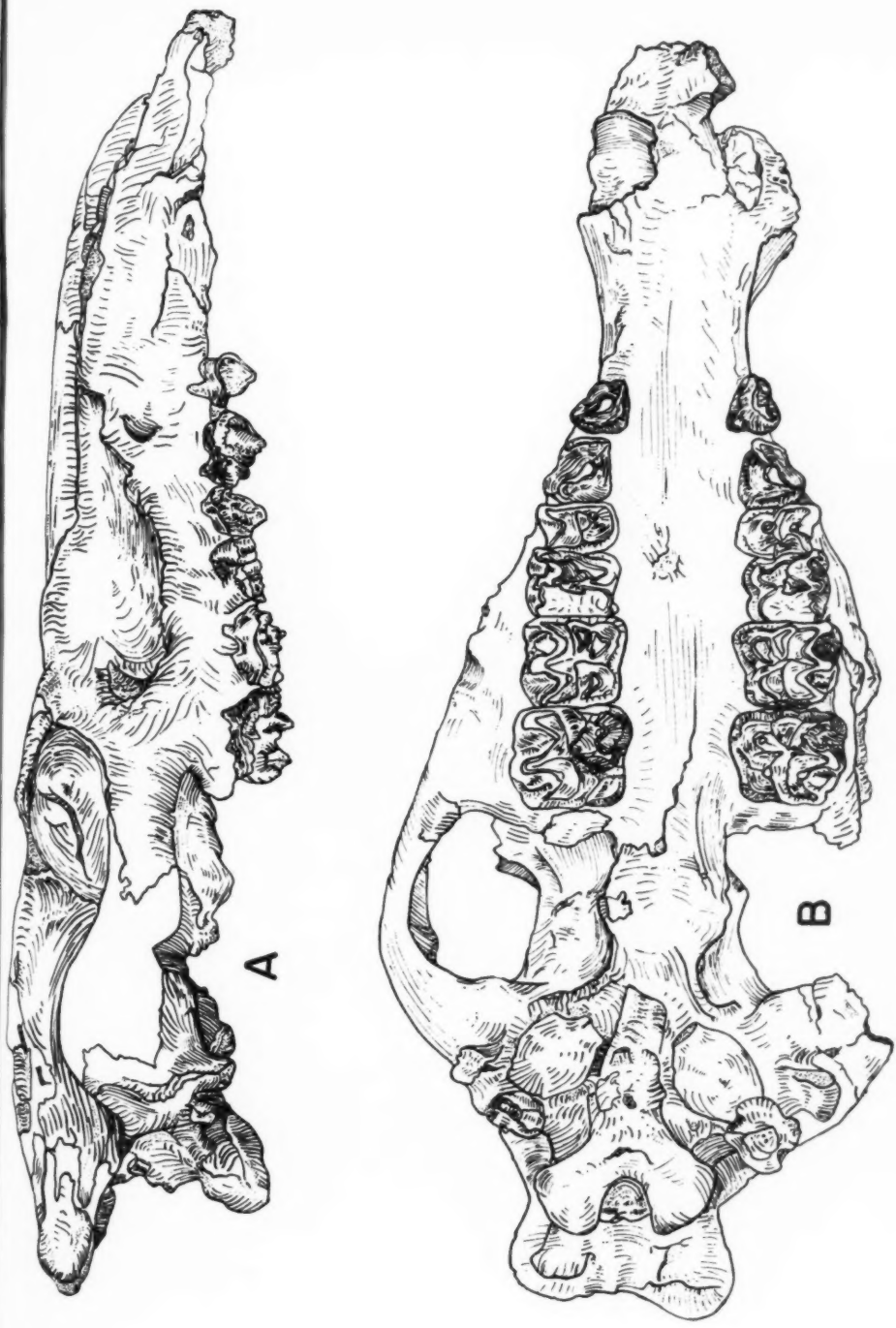
Ancodon brachyrynchus (Osborn & Wortman). GREGORY, 1920, Am. Mus. Nat. Hist., Bull., vol. 42, p. 190, fig. 162.

Hyopotamus brachyrynchus (Osborn & Wortman). O'HARRA, 1920, South Dakota Sch. Mines, Bull., vol. 13, p. 122, 154, fig. 60–61.

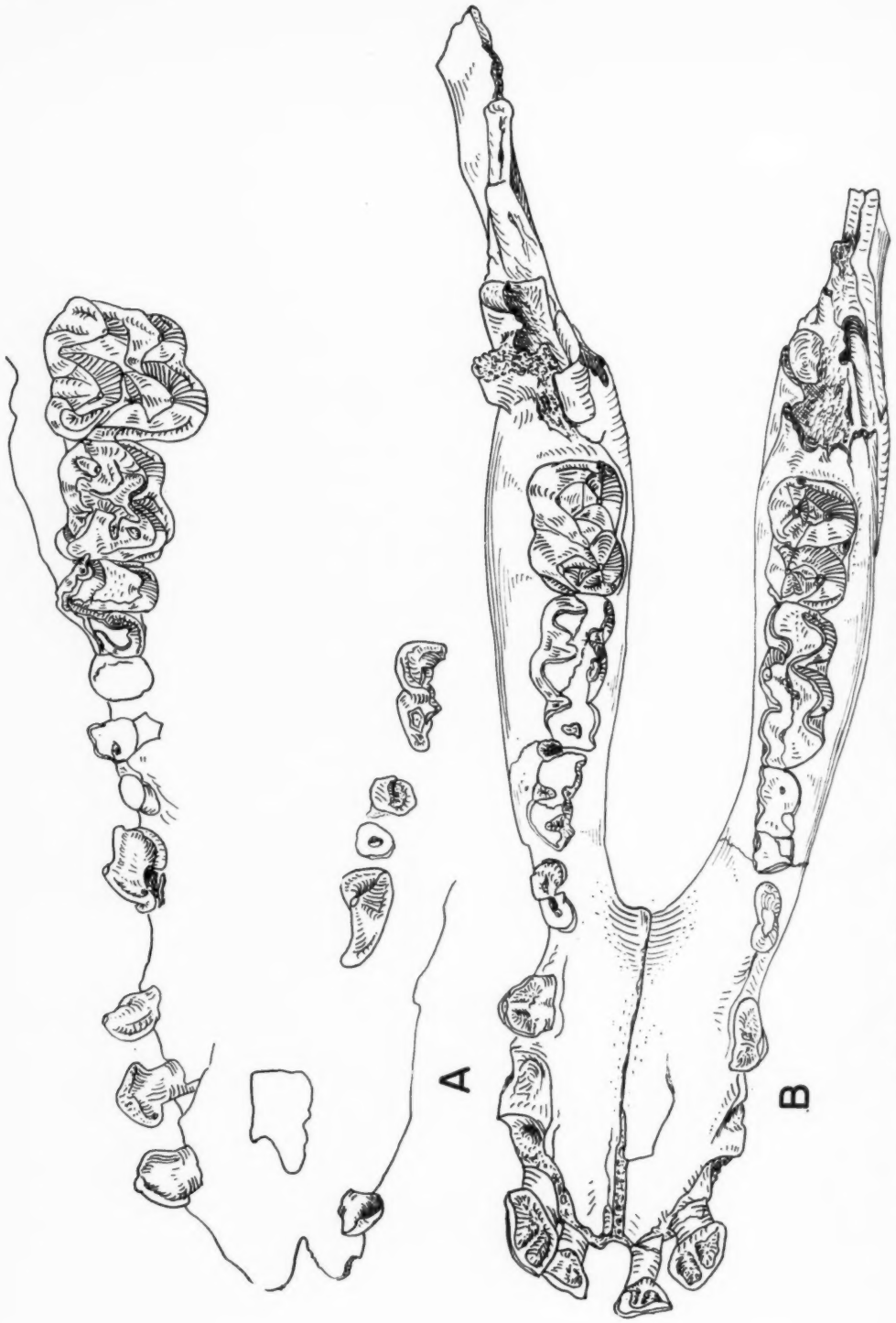
Ancodus brachyrynchus (Osborn & Wortman). WOODWARD, 1923, A guide to the fossil mammals [etc.], p. 38, fig. 21.

Elomeryx brachystylus (Osborn & Wortman). TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 333.

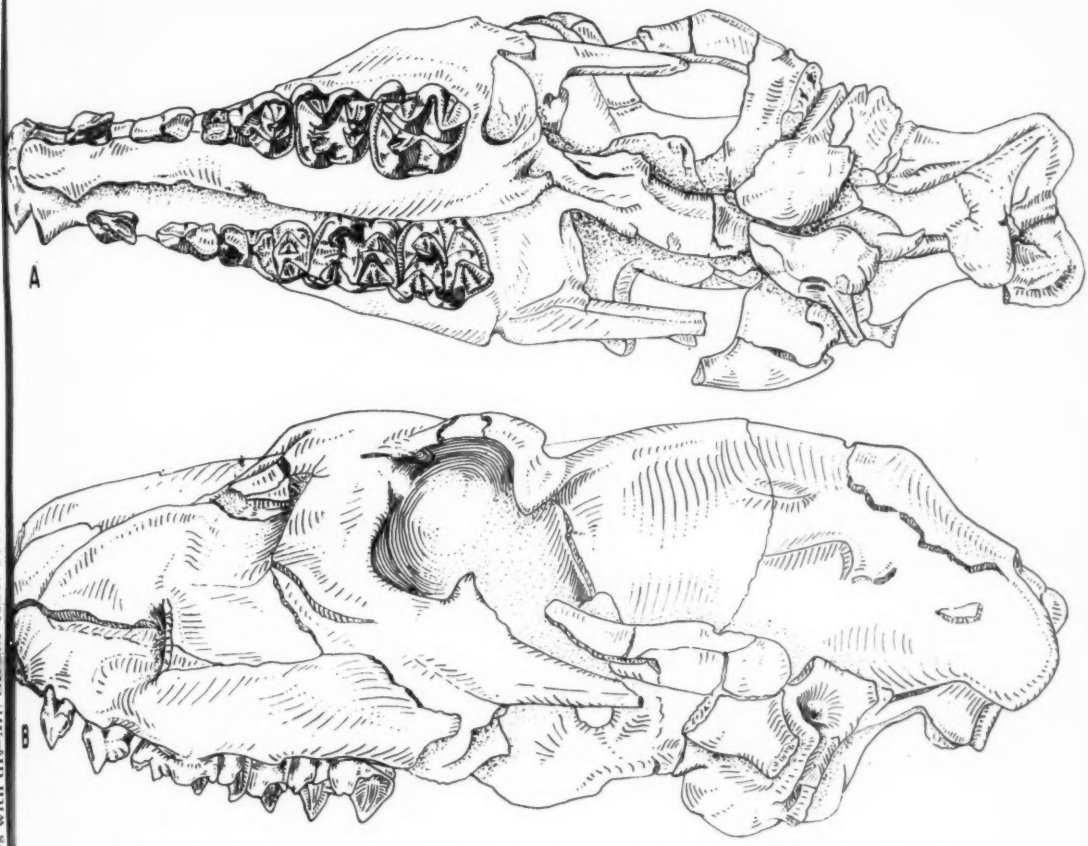
Brachyodus brachyrynchus (Osborn & Wortman).



TEXT-FIG 4.—*Elomeryx armatus*, female cranium: *A*, lateral view; *B*, occlusal view. SDSM 2841. ×½.



TEXT-FIG. 5—*Elomeryx armatus*, juvenile skull, cranium badly crushed; *A*, palate with dP4–M1; *B*, lower jaws with dP4–M1. SDSM 4084. ×1.



TEXT-FIG. 5—*Elomeryx armatus*, juvenile skull, cranium badly crushed; *A*, palate with dI²–M¹; *B*, lower jaws with dI₂–M₁. SDSM 4084. ×½.

TEXT-FIG. 6—*Elomeryx armatus*, juvenile cranium with dP¹–M¹: *A*, occlusal view; *B*, lateral view. SDSM 4012. ×¾.

WEBER & ABEL, 1928, Die Säugetiere, p. 540, 542, fig. 362.

Bothriodon brachyrhynchus (Osborn & Wortman). SCOTT, 1937, A history of the land mammals of the western hemisphere, p. 383.

Elomeryx brachyrhynchus (Osborn & Wortman). SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 473–475, pl. XLVII–XLIX.

Elomeryx armatus angustus Troxell. TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 334, fig. 5. HAY, 1930, Carnegie Inst. Washington, Pub. 390, p. 759. SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 472.

Type.—Partial skull. YPM 10176.

Type figure.—Marsh, 1894b, fig. 2.

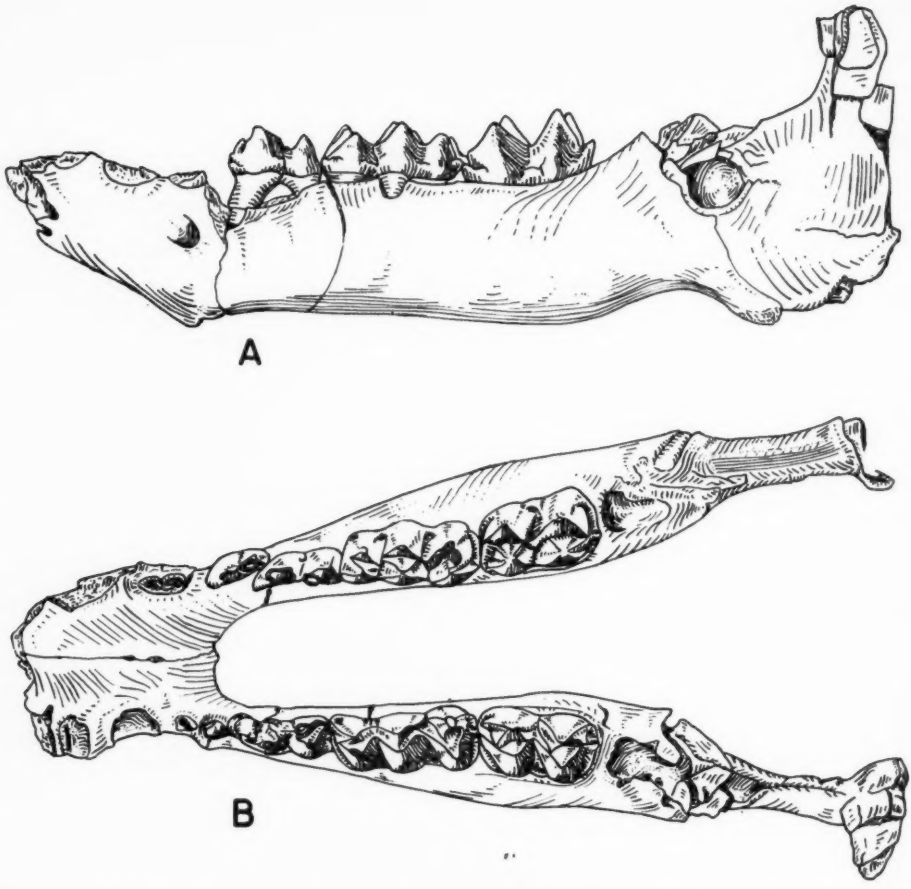
Type locality.—Big Badlands, South Dakota.

Horizon.—Protoceras channels, Poleslide member, Brule formation.

Age.—Whitneyan.

Diagnosis.—M^{1-3} with strong anterior and posterior cinguli, M^1 with strong parastyle, P^4 with protocone and paracone connected by posterior spur, protocone with rounded lingual face, strong cingulum sometimes broken over lingual face of protocone.

Discussion.—This species has been divided into three species and two subspecies by various authors. Marsh (1894b, p. 93) originally referred *E. armatus* to *Heptacodon* but later in the same year (1894c, p. 176) erected the genus *Elomeryx* with *E. armatus* as the type species of the genus. At the same time he described *E. mitis*, the type of which proved to be a juvenile with deciduous teeth. During the same year, the high-water mark in anthracotherian descriptions, Osborn and Wortman (1894, p. 220) described *Hyopotamus brachyrhynchus* which was later referred to *Ancodus* by Scott (1894, p. 294), was considered a synonym of *E. armatus* by Troxell (1921, p. 333), and reestablished by



TEXT-FIG. 7—*Elomeryx armatus*, juvenile lower jaws with dP_2–M_1: *A*, lateral view; *B*, occlusal view. SDSM 285. ×½.

Scott (1940, p. 473) as *Elomeryx brachyrhynchus*.

Troxell (1921, p. 334) divided *E. armatus* into two subspecies in his review of the American Bothriodonts; the variant being *E. armatus angustus*. This division was retained by Scott (1940, p. 472) in his review of the group.

In common with the other of North American anthracotheres there is a great deal of individual variation within this group. I believe that all of the described forms actually are variants within a single population. With one exception; namely, a maxillary fragment with dP^{3-4} from the Sespe of California (Stock, 1935, p. 124) all of the New World occurences of this form are from the Protoceras channels of the Big Badlands of South Dakota. As the channels represent a very limited geologic horizon and are found in a very restricted area it seems unlikely that there would be more than one species, let alone two subspecies of *Elomeryx*, in these deposits.

The characteristics used by Troxell to distinguish between the two sub-species certainly are individual variations in an extremely variable group of animals. Troxell (1921, p. 333) indicated a belief that *E. brachyrhynchus* (Osborn and Wortman) probably was based on a sexual variation rather than on the differences between two distinct species. Scott (1940, p. 471) considered these forms as two distinct species

distinguished by the position of the incisors, the size of the canines, and the position and size of the diastemas. He stated (p. 473–474),

> In the latter [*E. armatus*] the six incisors are curved in a semicircle, while in *E. brachyrhynchus* they are in a nearly straight line, those of the two sides being parallel; i3/ is isolated by a short space before and a longer behind, between it and the canine. In *E. armatus* there is a short space between i3/ and the canine.

An examination and comparison of the specimens now available in the various museums suggests that these differences are primarily sexual rather than specific. The individuals that have the characteristics of *E. armatus* have large canines which influence the entire shape of the snout and actually make the elongation of the muzzle more apparent than real. This can be readily seen in Text-fig. 3,4.

On the basis of this comparison it is concluded that the various species which have heretofore been described from the North American Oligocene are actually based on individual variation and sexual dimorphism.

Lower Jaws
Table of Measurements (mm.)

	SDSM 2859 Right	SDSM 2859 Left	PU 10653 Left
I_3, A-P diam.		12.4	
I_3, Tr diam.		8.0	
Diastema, I_3—Canine		2.0	
C, A-P diam.	11.8[1]	10.7[1]	
C, Tr diam.	6.1[1]		
Diastema, Canine—P_1	21.2	21.0	27.5
P_2 A-P diam.	12.5	13.2	12.5
P_2 Tr diam.	6.4	6.6	7.4
P_3 A-P diam.	17.2	17.2	17.7
P_3 Tr diam.	8.6	8.5	9.5
P_4 A-P diam.	20.2	19.4	20.5
P_4 Tr diam.	12.3	12.5	12.0
M_1 A-P diam.	19.3	20.6	15.3
M_1 Tr diam.	13.7	13.7	10.8
M_2 A-P diam.	27.5	27.5	24.1
M_2 Tr diam.	18.9	18.4	17.9
M_3 A-P diam.	44.4	44.8	41.1
M_3 Tr diam.	21.2	21.0	18.9
Canine—M_3	174.4	172.4	
P_2–M_3	139.3	140.8	
P_{2-4}	50.8	50.4	
M_{1-3}	90.0	90.7	

[1] alveoli

ELOMERYX sp.

(?) *Bothriodon* cf. *brachyrhynchus* (Osborn & Wortman). STOCK, 1935, Carnegie Inst. Washington, Pub. 453, p. 124, pl. 1, fig. 2.

The dP^{3-4} (CIT 1722) described by Stock (1935, p. 124) from the Kew Quarry is indistinguishable from several specimens of immature *Elomeryx armatus* from the Protoceras channels of the Big Badlands. While there is a great similarity between the upper cheek teeth of *Aepinacodon* and *Elomeryx* it is reasonable to assume that this specimen is referable to *Elomeryx*, and most likely to *Elomeryx armatus*.

Genus HEPTACODON Marsh

Heptacodon Marsh. MARSH, 1894a, Am. Jour. Sci., vol. 47, p. 409.
Octacodon Marsh. MARSH, 1894c, Am. Jour. Sci., vol. 48, p. 178.
Anthracotherium Osborn & Wortman (nec Cuvier), 1894, Am. Mus. Nat. Hist., Bull., vol. 6, p. 221–223.

Type species.—*Heptacodon curtus* Marsh.

Range.—Early to late Oligocene, North America.

Diagnosis.—Upper molars with transverse valley which does not enter mesostyle; parastyle, mesostyle and metastyle (if present) strongly developed as "prominent buttresses with conical summits." (Marsh, 1894B, p. 92); P_{1-3} simple; no diastema.

Discussion.—*Heptacodon* Marsh (1894A, p. 409) presents one of the most interesting examples of variation among the North American Anthracotheres. There have been five species described for this genus and one species described for *Octacodon* Marsh, which is herein considered a synonym of *Heptacodon*. Of these six species, four have been based on one or two isolated upper cheek teeth. One of these, *H. curtus* Marsh, the type species, is based on a dP^4 and another, *H. quadratus* Scott, is based on two M^1's and a dP^4.

This genus is quite distinctive with its short muzzle, heavily styled upper molars, simple anterior premolars and generally rounded and non-angular cusps on both the upper and lower teeth. The size of the canines is influenced by the sex of the individual as in *Elomeryx*.

HEPTACODON QUADRATUS Scott

Heptacodon quadratus Scott. SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 489, pl. LI, fig. 3.

Table of Measurements (mm.)

	Type YPM 10176	Plesiotype YPM 10195		*E. angustus* YPM 10393		*E. brachyrhynchus* AMNH 582	YPM 10352		KU 2779		USNM 5924		PU 10653	PU 12755		PU 12756		SDSM 2841		SDSM 40133	
		Right	Left	Right	Left	Right	Right	Left	Right	Left	Right	Left	Right	Right	Left	Right	Left	Right	Left	Right	Left
I^1 A-P diam.													12.9								
I^2 Tr diam.													7.5								
I^3 A-P diam.													10.8								
I^3 Tr diam.													7.4								
Diastema, I^3—Canine													15.2								
C/ A-P diam.													9.3							17.2	
C/ Tr diam.													8.2							11.2	
Diastema, Canine—P^1										38.4			24.7			18.2	20.6			29.3	
P^1 A-P diam.				19.4[1]	11.9[1]				13.3	15.7	12.35		9.7							8.5	
P^1 Tr diam.											6.5		5.8							6.5	
Diastema P^1–P^2													8.8							5.4	
P^2 A-P diam.				15.9		15.7	17.3		14.9	14.9	17.1		17.0	17.4	16.7			13.7	13.3	14.6	14.4
P^2 Tr diam.				9.5		10?4	12.1		11.1		11.3		11.8	11.1	10.7			10.7	10.8	9.5	9.7
P^3 A-P diam.	18.2			20.7		19.5	20.3	19.2		17.5	19.7	19.8	19.6	19.5	19.6	20.6	20.6	18.7	18.1	18.9	18.9
P^3 Tr diam.	16.7			14.9		16.4	17.5			18.2	17.5	17.8	16.7	16.3		?15.5	15.4	15.8	15.5	14.5	15.3
P^4 A-P diam.	14.3			14.7		14.8	15.3	15.2		12.9	15.2	15.5	14.4	14.6	14.2	15.4	15.4	14.7	14.6	13.8	13.8
P^4 Tr diam.	19.5			20.0		19.1	19.6			19.3	19.8	20.4	22.5	19.8	17.3	19.8	19.7	20.5	20.6	19.2	19.0
M^1 A-P diam.	19.8			21.4		20.0	18.8	18.4		17.8		17.4	?17.2	19.9		20.0	19.0	18.4	18.7		
M^1 Tr diam.	22.3			21.6	21.2	20.8	22.4					22.4	24.8	20.1		22.8		21.4	20.7		
M^2 A-P diam.	27.0		28.3	26.0		26.3	25.1	25.0		26.1	26.9	26.3	24.1	26.3	25.6	26.5	26.5	24.3	23.8	24.4	
M^2 Tr diam.	28.8		28.6	27.0	26.6	26.0	26.5			28.5	27.8	27.8	29.2	25.7	25.7	28.8		26.7	26.5	27.7	
M^3 A-P diam.	30.5	31.0	31.4	32.4	32.0	28.4	29.5	28.8		30.5	31.0	31.2	30.0	30.0	30.0	28.5		27.6		29.3	29.0
M^3 Tr diam.	33.4	32.6	33.0	33.6	33.3	29.3	30.8	30.8		33.7		32.4	32.4	29.7	30.7	34.9	33.5	30.8		32.5	32.9
Greatest length, Canine—M^3													175.8							174.9	
Greatest length, P^1–M^3											135.0		142.5			137.5				131.4	
Greatest length, P^1–4											62.1									62.5	
Greatest length, M^1–3	76.6			78.1	76.9	73.0	70.2	68.5		73.6	72.9	72.3	71.2			72.0		69.5	69.4	69.7	70.0

[1] alveoli

Juveniles
Table of Measurements (mm.)

	E. mitis (Type)	SDSM 4084 Right	SDSM 4084 Left	SDSM 2862 Right	SDSM 2862 Left	SDSM 4012 Right	SDSM 4012 Left	SDSM 285 Right	SDSM 285 Left	CIT 1722
dI^2 A-P diam.		7.5	7.8							
dI^2 Tr diam.		4.2	4.4							
dI^3 A-P diam.		6.3								
dI^3 Tr diam.		3.3								
dC A-P diam.		7.0								
dC Tr diam.		4.4								
dP^1 A-P diam.		11.5	12.3			10.8	11.4			
dP^1 Tr diam.		6.3	7.1			5.2	5.3			
dP^2 A-P diam.						12.4	13.2			
dP^2 Tr diam.						5.8	5.2			
dP^3 A-P diam.	19.9	19.1		19.8	19.5	18.0	18.8			
dP^3 Tr diam.	13.0	14.7		15.0	14.4	13.2	12.8			
dP^4 A-P diam.	17.0	17.0		18.2	18.2	17.3	17.2			17.4
dP^4 Tr diam.	16.4	17.5		18.2	18.3	16.2				15.4
M^1 A-P diam.	21.2	20.2		22.0	22.0	20.8	21.1			
M^1 Tr diam.	20.0	20.8		22.5	22.3	19.7				
M^2 A-P diam.	26.8				26.4					
M^2 Tr diam.	25.6									
dI_2 A-P diam.		10.5	11.3							
dI_2 Tr diam.		4.6	4.5							
dP_1 A-P diam.		9.6	9.5							
dP_1 Tr diam.		4.2	4.2							
dP_2 A-P diam.									10.5	
dP_2 Tr diam.									4.5	
dP_3 A-P diam.		15.6						14.7	15.2	
dP_3 Tr diam.		6.5						7.0	7.0	
dP_4 A-P diam.		24.5	23.8					24.4	24.4	
dP_4 Tr diam.		10.5	10.4					10.6	11.0	
M_1 A-P diam.		19.1	19.4					20.0	20.0	
M_1 Tr diam.		12.2	12.3					12.0	12.2	

Type.—Three upper cheek teeth including a dP^4 and two M^1's. PU. 10828.

Type locality.—Big Badlands, South Dakota.

Horizon.—Scenic member, Brule formation.

Age.—Orellan.

Type figure.—Scott, 1940, pl. LI, fig. 3.

Diagnosis.—Small size, wrinkled enamel, strong cingulum.

Discussion.—The characteristics enumerated above in the diagnosis are not sound specific characteristics among the highly variable anthracotheres. Actually, the only valid reason for retaining this species is the fact that it is so much smaller than the contemporaneous *H. occidentalis* (Osborn and Wortman). The M^1 resembles that of a cranium (UC 1795) at the Chicago Natural History Museum which is referable to *H. occidentalis*; but here again size might be important enough to separate these as distinct species. Although the Chicago specimen is smaller than the type, it is still larger than *H. quadratus*.

Scott (1940, p. 489) stated that the type consisted of a M^1 and two M^2's. However, the maxillary fragment containing the two right teeth is still attached to the anterior end of the jugal which terminates just above the posterior tooth. In other skulls referable to this genus this suture is just above the M^1 which suggests that the smaller anterior tooth in this pair is a dP^4. It might also be noted that the roots of dP^4 in a juvenile cranium of *H. valens* (SDSM 2875) are nearly as long as those of the M^1 and that the P^4 is deeply buried in the maxillary although the M^1 and the M^2 are fully erupted. In fact, the apex of the paracone of the P^4 is approximately 15 mm. above the plane of the occlusal surface.

Table of Measurements (mm.)

Type—PU 10828	Right	Left
dP^4 A-P diam.	16.0	
dP^4 Tr diam.	16.1	
M^1 A-P diam.	17.6	17.6
M^1 Tr diam.	18.8	18.1

HEPTACODON OCCIDENTALE (Obsorn & Wortman)

Anthracotherium curtum Osborn & Wortman. OSBORN & WORTMAN, 1894, Am. Mus. Nat. Hist., Bull., vol. 6, p. 221, fig. 6, 7.
Anthracotherium occidentale Osborn & Wortman. OSBORN & WORTMAN, 1894, idem., p. 223.
Octacodon cf. *gibbiceps*. TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 328.
Heptacodon occidentalis Scott. SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 483–485.

Type.—Partial skull. AMNH 1039.

Type locality.—Big Badlands, South Dakota.

Horizon.—Metamynodon channels, Scenic member, Brule formation.

Age.—Orellan.

Type figure.—Osborn and Wortman, 1894, figs. 6c and 7.

Diagnosis.—Small. M^3 with reduced metastyle. M^{1-3} with lingual cingulum missing over protocone and hypocone; cusps low. P^4 with well developed lingual cingula; compressed antero-posteriorly; protocone and paracone well separated, acute, protocone nearly as tall as paracone.

Discussion.—This species presents little in the way of problems of identification, but the synonymy is perhaps more complex than usual. Osborn and Wortman described this species in 1894 as *Anthracotherium occidentale*. Prior to publication, Marsh's description of *Heptacodon curtus* was issued. At this time, Osborn and Wortman altered their manuscript and referred their specimen to *Anthracotherium curtum* (Marsh). This was done on the two figures and on the section heading. However, the section on this specimen contains only a description of the specimen. At the end of the discussion of the two species of *Anthracotherium* there is a recapitulation of diagnostic characteristics headed "*A. occidentale.*"

Scott (1940), p. 483–484) discussed the pros and cons of this situation and resolved the problem by reviving the name *occidentale* and citing it as *Heptacodon occidentalis* nom. nov. While this is admirable from the point of view of the conservation of names it probably is not acceptable under the rules. In spite of the possibility of this name being unacceptable under the letter of the law it certainly is worthy of retention. The only point of conflict would be as to whether or not the name should be credited to Scott as the reviver in 1940 or to Osborn & Wortman as the inadvertent describers in 1894. As the name does appear in Osborn & Wortman (1894, p. 223) accompanied by a diagnosis, I believe that they should be credited with the name.

Except for size there is very little difference between the upper cheek teeth of *H. occidentale* and its larger successor *H. gibbiceps* Marsh from the late Oligocene.

This species differs from the other small species, *H. quadratus*, from the Orellan in that it has reduced cingula and lower cusps. These are not distinctive characteristics when the variation among individuals of other species is considered but, due to a lack of specimens from this horizon, these species may for the present be regarded as distinct.

Table of measurements (mm.)
After Scott, 1940, p. 484
Type specimen AMNH 1039

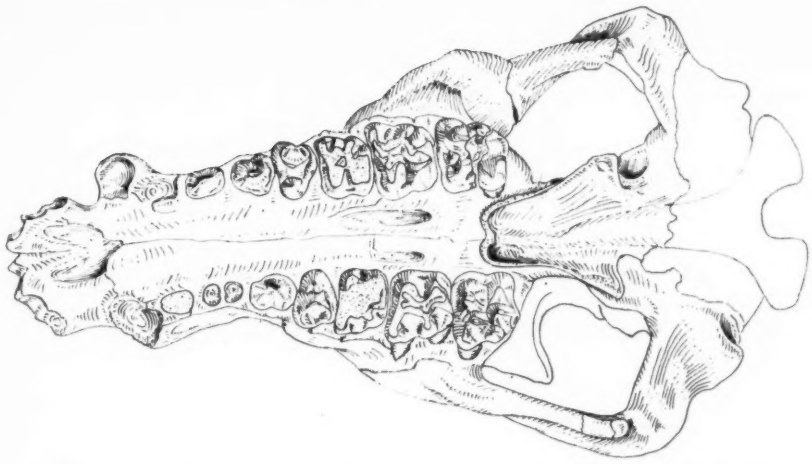
Upper canine, A-P diam.	16
Upper canine, Tr diam.	13
Upper cheek-tooth series, length P^2–M^3	98
P^2 A-P diam.	13
P^2 Tr diam.	8
P^3 A-P diam.	17
P^3 Tr diam.	12
P^4 A-P diam.	12
P^4 Tr diam.	15
Upper molar series, length	59
M^1 A-P diam.	19
M^1 Tr diam.	20.5
M^2 A-P diam.	21
M^2 Tr diam.	25
M^3 A-P diam.	23
M^3 Tr diam.	25

HEPTACODON GIBBICEPS Marsh
Text-fig. 8,9

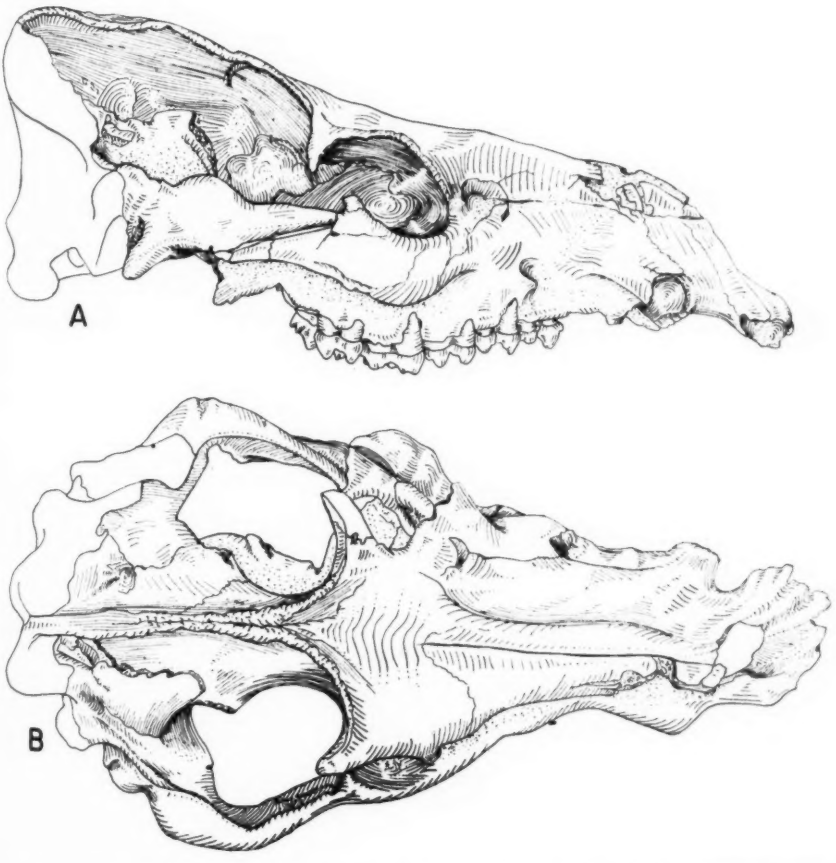
Heptacodon gibbiceps Marsh. MARSH, 1894c, Am. Jour. Sci., vol. 48, p. 175, fig. 2.
Anthracotherium gibbiceps (Marsh). MATTHEW, 1899, Am. Mus. Nat. Hist., Bull., vol. 12, p. 59. HAY, 1902. U. S. Geol. Survey, Bull. 179, p. 652.
Octacodon gibbiceps (Marsh). TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 329, fig. 3. HAY, 1930, Carnegie Inst. Washington, Pub. 390, p. 759.
Heptacodon gibbiceps Marsh. SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 486–489, pl. LI, fig. 1.

Type.—A rostrum with P^2–M^3. YPM 10194.

Type locality.—Big Badlands, South Dakota.



TEXT-FIG. 8—*Heptacodon gibbiceps*, cranium: palatal view. SDSM 2751. ×⅓.



TEXT-FIG. 9—*Heptacodon gibbiceps*, cranium: *A*, lateral view; *B*, dorsal view. SDSM 2751. ×⅓.

Horizon.—Protoceras channels, Poleslide member, Brule formation.[1]

Age.—Whitneyan.

Type figures.—Marsh, 1894C, fig. 2, and Troxell, 1921, fig. 3.

Diagnosis.—M^{1-3} with reduced metastyle; cingula not prominent, interrupted on lingual face of protocone; protocones, protoconules, and hypocones low and rounded. P^4 with lingual cingulum reduced or absent.

Discussion.—This species appears to be a direct descendant of *H. occidentale* (Osborn & Wortman). There has been no significant change in the dental pattern. The only apparent change is an increase in size. A fine cranium (SDSM 2751), lacking only the occipital and otic region, was figured by Scott (1940, pl. L) and referred to *H. karense* at that time. This same cranium formed the basis of his description of the skull of *Heptacodon*. This specimen (Text-fig. 8,9) is herein referred to *H. gibbiceps* as the dentition is virtually identical to that of the type.

Table of Measurements (mm.)

	YPM 10194		SDSM 2751	
	Right	Left	Right	Left
P^2 A-P diam.		16.4		14.3
P^2 Tr diam.		10.0		9.2
P^3 A-P diam.	18.3	17.8	16.9	17.0
P^3 Tr diam.	15.0	15.2	14.2	14.3
P^4 A-P diam.	14.8	16.7	15.4	15.8
P^4 Tr diam.	21.4	21.6	21.3	21.2
M^1 A-P diam.	22.6		21.3	20.9
M^1 Tr diam.			24.8	25.2
M^2 A-P diam.	25.7		24.8	25.8
M^2 Tr diam.			29.2	28.9
M^3 A-P diam.	24.8	26.0	24.8	
M^3 Tr diam.	32.8	32.8	30.3	30.0
Alveolus P^1–P^4		62.7	62.6	64.5
M^{1-3}		73.7	70.4	
Palatilar length			175.6	

[1] The locality is given by Troxell (1921, p. 329) for the type locality is "Upper Oligocene (Protoceras beds), Hermosa, South Dakota," and for *Heptacodon curtus* Marsh it is "Upper Oligocene (Protoceras beds), Phinney, South Dakota." The coupling of these localities with the Protoceras channels is a geographic impossibility as the nearest Protoceras channels to Hermosa are at Sheep Mountain Table or about six miles east of Rockyford, a distance of at least thirty miles to the nearest occurrence. If Phinney refers to the area that is now known as Phinney Flat, then a similar situation exists although the distance is perhaps only twenty miles. Presumably these were the locations of base camps or where the specimens were obtained from settlers or Indians. The horizon seems to be correct because referable material in the Museum of Geology does come from the Protoceras channels.

HEPTACODON CURTUS Marsh
Text-fig. 10,11

Heptacodon curtus Marsh. MARSH, 1894a, Am. Jour. Sci., vol. 47, p. 409. MARSH, 1894, ibid., p. 176, fig. 1.

Anthracotherium curtum (Marsh). MATTHEW, 1899, Am. Mus. Nat. Hist., Bull., vol. 12, p. 58. HAY, 1902, U. S. Geol. Survey Bull., 179, p. 652. MATTHEW, 1901, Am. Mus. Nat. Hist., Mem., 1, p. 369. MATTHEW, 1909, U. S. Geol. Survey Bull., 361, p. 106. COOK, 1912, Nebraska Geol. Survey, vol. 7, p. 37.

Heptacodon curtus Marsh. TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 327, fig. 1. HAY, 1930, Carnegie Inst. Washington, Pub. 390, p. 759. SCOTT, 1940, Am. Philos. Soc. Trans., vol. 28, p. 482–483.

Anthracotherium karense Osborn & Wortman. OSBORN & WORTMAN, 1894, Am. Mus. Nat. Hist., Bull., vol. 6, p. 222, fig. 8. MATTHEW, 1899, Am. Mus. Nat. Hist., Bull., vol. 12, p. 59. HAY, 1902, U. S. Geol. Survey, Bull. 179, p. 652. MATTHEW, 1909, U. S. Geol. Survey Bull., 361, p. 109. COOK, 1912, Nebraska Geol. Survey, vol. 7, p. 39. O'HARRA, 1920, South Dakota Sch. Mines, Bull., vol. 13, p. 154.

Octacodon karense (Osborn & Wortman.) TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 328.

Anthracotherium karense Osborn & Wortman. HAY, 1930, Carnegie Inst. Washington, Pub. 390, 758–759. SCOTT, 1940, Am. Philos. Soc. Trans., vol. 28, p. 485–486, pl. 50.

Octacodon valens Marsh. MARSH, 1894b, Am. Jour. Sci., vol. 48, p. 92, fig. 1. MARSH, 1894, ibid., p. 178, fig. 6. MATTHEW, 1899. Am. Mus. Nat. Hist., Bull., vol. 12, p. 59.

Octacodon valens Marsh. HAY, 1902, U. S. Geol. Survey Bull., 179, p. 652. TROXELL, 1921, Am. Jour. Sci., vol. 1, p. 328, fig. 2. HAY, 1930, Carnegie Inst. Washington, Pub. 390, p. 759. SCOTT, 1940, Am. Philos. Soc., Trans., vol. 28, p. 490–492, pl. XLIX.

Type.—A dP^4. YPM 2232.

Type locality.—Big Badlands, South Dakota.

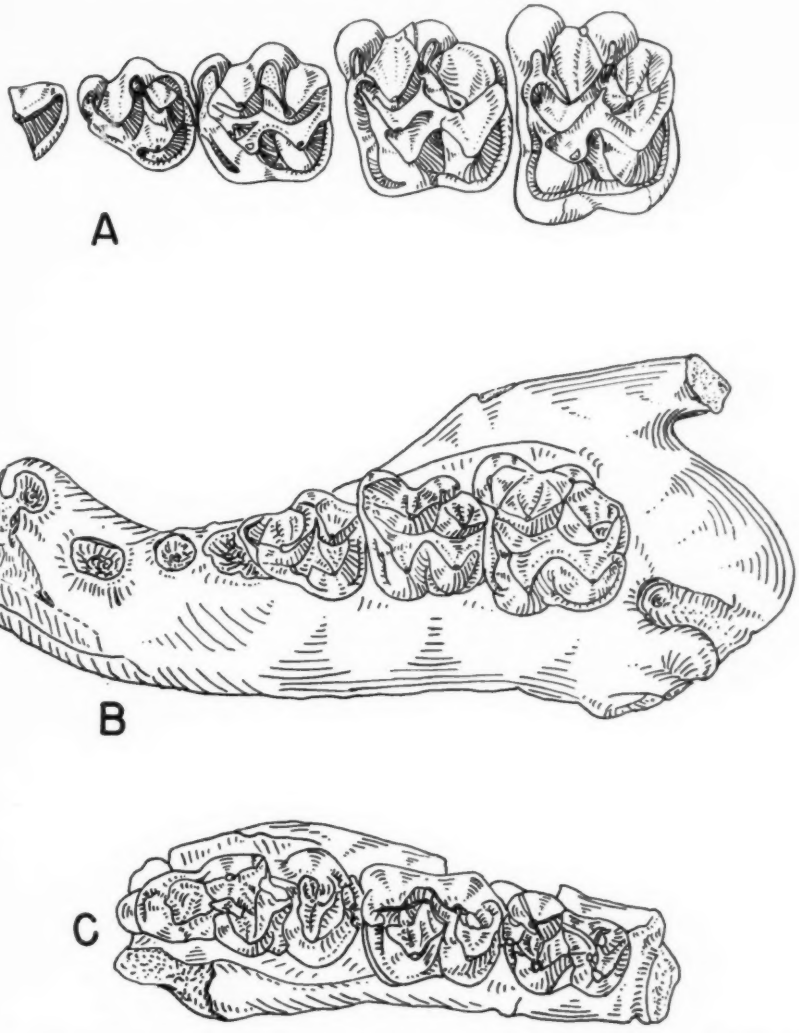
Horizon.—Protoceras channels, Poleslide member, Brule formation.

Age.—Whitneyan.

Type figure.—Marsh, 1894A, fig. 1.

Emended diagnosis.—M^{1-3} with prominent sharp cusps, protoconule prominent, parastyle and mesostyle prominent and hypertrophied, cingulum highly variable; M^3 with prominent metastyle; P^4 with reduced protocone.

Discussion.—This species is represented by perhaps a dozen specimens, all from the Protoceras Channels of the Big Badlands. These specimens have been distributed among three species based on minor differences in size, cusp shape, and the size and



TEXT-FIG. *10*—*Heptacodon curtus* (*A* and *B*) and *Heptacodon* sp. (C): *A*, P^2–M^3, SDSM 2875; *B*, dP^2–M^1, UC 1795; *C*, jaw fragment with M1–3. CM 14577. ×1.

position of the cingula of the upper molars. This was justifiable, in part, due to the lack of complete dentitions and the fact that the types of the various species seem to represent extremes in variation. As all the material comes from a very limited horizon and small geographic area, it seems unlikely that there actually is more than one species represented.

Two partial crania are now available which are referable to this species. In conjunction with the types of *H. curtus*, *H. karense*, and *Octacodon valens* the dentitions of these crania may be placed in a continuous series indicating variation within a single species.

The three species that are referred to *H. curtus* are listed below with the data regarding the types and their definitions.

Heptacodon curtus Marsh, April, 1894

Type.—A dP^4. YPM 2232.

Troxell (1921, p. 328) distinguished this from the other species as follows,

—absence of cingulum except on the anterior side; the bases of the protocone and hypocone equal; these two cones joined by two ridges inclosing a deep short segment of the transverse groove; the proto-conule weak; the para- and metacones most prominent of all the moderate cones; ridges from them joining one from the mesostyle to form a Y as in *Octacodon*: the parastyle very prominent, with a sharp cusp, and widely separated from the mesostyle; the metastyle almost obsolete.

Anthracotherium karense Osborn & Wortman, July, 1894

Type.—A maxillary fragment with M^{2-3}. AMNH 1040.

The mesostyles are broken away on these two molars, which alters their appearance a great deal. Osborn and Wortman (1894, p. 223) defined the species as follows,

Formula unknown. Cusps of molars elevated and crescentic, Mesostyle a prominent crested spur. Metastyle very prominent in $M._3$. Measurements: $M._{2-3}$, 54 mm. Width, $M._3$, 27 mm.

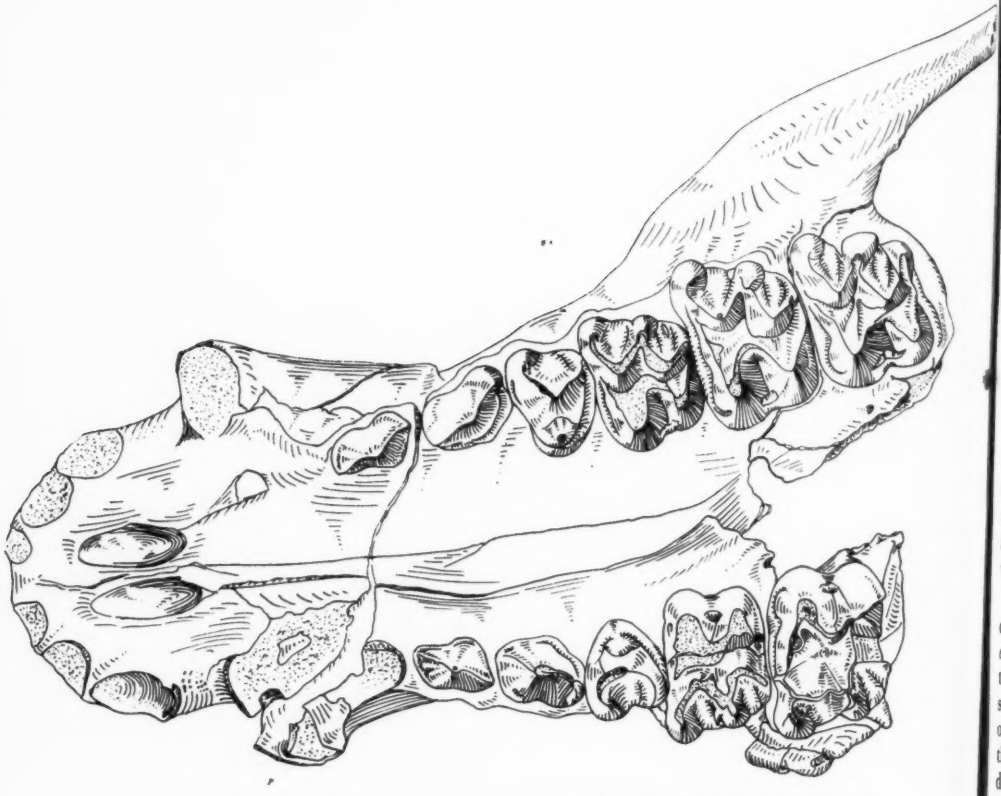
Octacodon valens Marsh, August, 1894b.

Type.—A M^3. PYM 11860.

This single tooth formed the type not only for the species but, in reality, for the genus *Octacodon*. Troxell (1921, p. 329) distinguished the species in the following manner,

The low cusps, absence of cingula excepting a weak one anteriorly, the prominence of the three styles, and especially the para- and mesostyles, the shallowness of the transverse valley which ends between the para- and metacone, the distinct ridge from the cusp of the mesostyle forming a Y with ridges from the para- and metacones, the short antero-posterior and great transverse diameter anterior, and the general smoothness, are all features which separate the species from those of any other genus.

Additional material now available to supplement the types of these species shows that they all appear to represent variants



TEXT-FIG. *11*—*Heptacodon curtus*, palate with P^2–M^3. SDSM 4023. $\times\frac{2}{3}$.

of the same species. The dentition of one cranium (SDSM 2875) closely resembles that of the type of *H. karense* while its dP^4 is similar, although not identical, to the type of *H. valens*. This dP^4 along with the dP^4 in a cranium from the Orellan of Hat Creek, Nebraska (UC 1795, see Text-fig. 10) probably *H. occidentale* although there is no positive indication of affinity other than age, indicates the general characteristics of dP^4's in this genus and shows that the type of *H. curtus* is a deciduous tooth. The other specimen from the Protoceras channels (SDSM 4023, Text-fig. 11) consists of a rostrum with the alveoli of the incisors, the canines, and the P^1, and the remainder of the dentition complete and well preserved. These cheek teeth closely resemble those of *O. valens*.

When these specimens are considered and studied as a unit the continuity of variation is readily seen and it is immediately apparent that these species actually are variations within a single group.

The type of *H. curtus* was considered by Marsh (1894a, p. 409) to be a M^3. Both Troxell (1921, p. 327) and Scott (1940, p. 738) concluded that it was an M^2. A comparison with the dP^4 of SDSM 2875 from the Protoceras channels suggests that this tooth is really a dP^4. This is indicated by the smoothness of the enamel, the relatively small size of the protoconule, and the regularity of the enclosed diamond shaped segment of the transverse valley between the protocone and the hypocone. These characteristics are approximated in the juvenile skull from Hat Creek, Nebraska, mentioned above.

However, in both the South Dakota and Nebraska skulls, the dP^4's are longer along the lingual border than the type. This may again be individual variation as the great amount of variation in the other teeth would seem to indicate.

Anthracotherium karense represents a moderately heavily cingulated variant of *H. curtus*. The M^2 of the type closely matches the M^2 of SDSM 2875, which is slightly smaller and whose cingulum is continuous over the protocone. M^3 is not present in this cranium (SDSM 2875) as exploratory digging revealed that it had not formed, although the other molars were fully erupted and the anterior surfaces of the anterior cusps of M^1 were beginning to wear. It might be argued that *A. karense's* large metastyle would set this species apart. However, the M^3 of cranium SDSM 4023 does have a well developed metastyle while there is no sign of this cusp on the M^1 and M^2. This may well be a distinguishing characteristic of this species as the other forms with known M^3's do not have well developed metastyles.

The type of *Octacodon valens* Marsh, an isolated M^3 (YPM 11860), presents an extreme example of the hypertrophy of the stylar cusps. This condition is almost attained in the M^3 of the type of *M. karense* although the metastyle, while equally as large, has grown posteriorly rather than labially.

The rostrum, SDSM 4023, has teeth which stand between the type of *A. karense* and *O. valens* in the development of the cingula. These are smaller than in the former and more prominent than in the latter. The stylar cusps are smaller than in either of the types.

In view of the relatively small sample of *Heptacodon* specimens now available and in light of the fact that all of these specimens discussed in the preceding paragraphs were found within a limited geographic and geologic range, it seems logical to include all of this material in the species *H. curtus* Marsh. The validity of this arrangment is further strengthened by the great range in variation found in *Elomeryx armatus*, the most abundant anthracothere in the Protoceras channels.

HEPTACODON sp.
Text-fig. 12

A pair of mandibles (SDSM 53309) from the Yoder locality, Goshen County, Wyoming; of earliest Chadronian age represents the oldest record of an Anthracothere in the New World. The tooth row is straight, the canine is small and the symphysis does not have an anterior flare as does the jaw (AMNH 1360) that Scott (1940, p. 484–485, pl. LI, fig. 2,2a) referred to *H. curtus*, and another pair of lower jaws (UKMNH 2581) from an unknown horizon in the Big Badlands.

The Yoder jaws may represent a nontusked form or, again, it may be a case of sexual dimorphism and consequently female.

Table of Measurements (mm.)

SDSM 53309	Right	Left
Canine A-P diam.	9.8	
Canine Tr diam.	7.7	
P_1 A-P diam.		7.6
P_1 Tr diam.		5.0
P_2 A-P diam.	11.7	11.3
P_2 Tr diam.	6.0	6.0
P_3 A-P diam.		14.5
P_3 Tr diam.	7.5	7.4
P_4 A-P diam.	unmeasurable	
P_4 Tr diam.	9.3	9.4
M_1 A-P diam.	17.7	17.3
M_1 Tr diam.		11.8
M_2 A-P diam.	20.2	19.3
M_2 Tr diam.	?14.4	14.4
Canine—M_2, total length	107.8	

HEPTACODON sp.

Heptacodon occidentalis Scott, SCOTT, 1940, Am. Philos. Soc., Trans. vol. 28, p. 484–485.
Heptacodon curtus Marsh. SCOTT, 1940, ibid., pl. LI, fig. 2,2a.

A mandible (AMNH 1360) from the Scenic member of the Brule formation, Big Badlands, South Dakota was figured and described by Scott (1940). It is indeterminate, but Scott (1940, p. 485) referred it to *H. occidentalis* Scott as it came from the same horizon as the type of *H. occidentale* Osborn and Wortman. This seems to be a reasonable assumption, but should be listed separately until associated material has been discovered.

Table of Measurements (mm.)

	AMNH 1360 (After Scott)	UKMNH 2581	
Lower dentition, I_1–M_3	154		
Lower canine alveolus A-P diam.	14		
Lower cheek-tooth series, length	125	123.5	
Lower premolar series, length	58		
P_2 A-P diam.	12.5	9.9	
P_2 Tr diam.	7		
P_3 A-P diam.	15	13.85	
P_3 Tr diam.	8		
P_4 A-P diam.	17	13.3	
P_4 Tr diam.	11		
Lower molar series, length	67	67.4	67.5
M_1 A-P diam.	18	18.2	18.8
M_1 Tr diam.	13	12.2	11.9
M_2 A-P diam.	19	20.8	20.1
M_2 Tr diam.	16	14.6	14.6
M_3 A-P diam.	29	28.2	28.2
M_3 Tr diam.	16	14.3	14.5
Mandible, length from condyle	215		
Mandible, depth at P_1	35		
Mandible, depth at M_3	38		
Mandible, thickness at M_2	22		

HEPTACODON sp.

A pair of mandibles (UKMNH 2581) collected by E. C. Case in 1894, are recorded from Custer County, South Dakota. Custer County is now the north half of Fall River County, but the specimen probably was actually collected on the southeast side of the Cheyenne River on Indian Reservation land just over the county line. There is no indication as to the age, but it probably is from the Orellan Scenic Member of the Brule. The measurements are given above. There is no essential difference between this specimen and AMNH 1360 except that the talonid of M_3 is somewhat narrower.

HEPTACODON sp.

A jaw fragment with M_{1-3} (UM 14577) from the Chadron formation north of Weta, Jackson County, South Dakota is indeterminate but is not greatly unlike the jaws from the Yoder.

Table of Measurements (mm.)

UM 14577	
M_1 A-P diam.	18.5
M_1 Tr diam.	12.2
M_2 A-P diam.	20.5
M_2 Tr diam.	14.6
M_3 A-P diam.	?30.4
M_3 Tr diam.	?15.5
Total length, M_{1-3}	69.3

HEPTACODON sp.

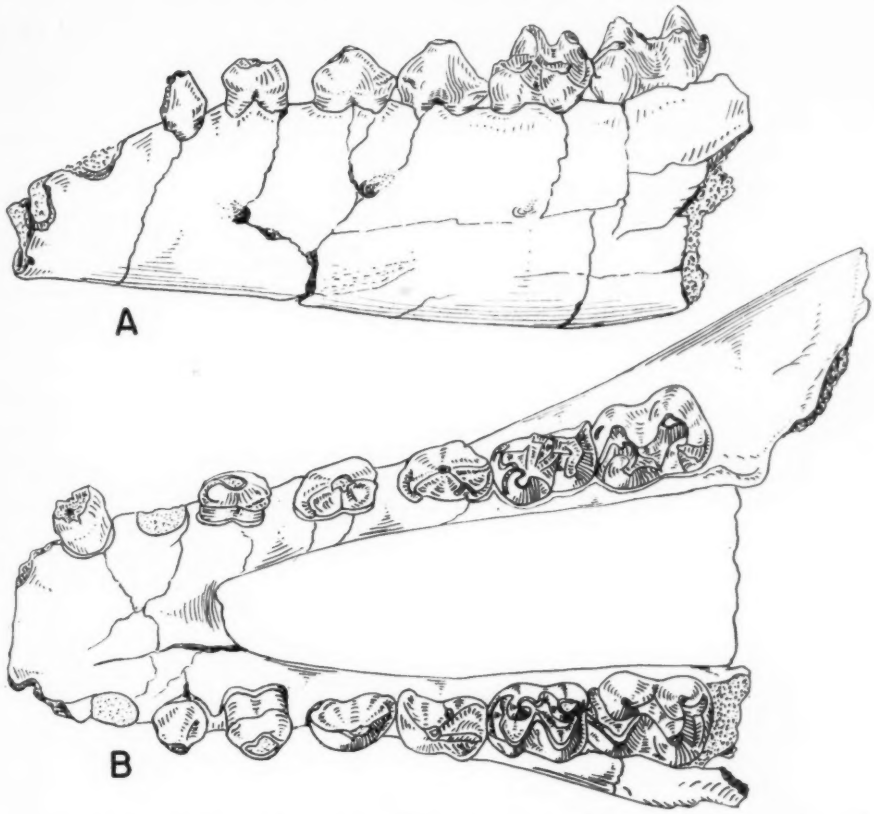
Heptacodon sp. GALBREATH, 1953, Univ. Kansas Paleont. Contr., vol. 4, p. 86.

A left mandible (UKMNH 8235) from the Cedar Creek member of the White River formation in Logan County, Colorado, was referred to *Heptacodon* sp. by Galbreath (1953, p. 86). This jaw is not unlike the jaw (AMNH 1360) from the Big Badlands, which is herein also referred to *Heptacodon* sp.

Genus ARRETOTHERIUM Douglass

Arretotherium DOUGLASS, 1901, Am. Philos. Soc., Trans., vol. 20, p. 269.

Type species.—Arretotherium acridens Douglass.



TEXT-FIG. *12*—*Heptacodon* sp., lower jaws with Canine—M_2: *A*, lateral view; *B*, occlusal view. SDSM 53309. ×⅔.

Range.—Early and middle Miocene, North America.

Diagnosis.—Short rostrum without diastema, upper cheek teeth as in *Elomeryx* except molars have lost protoconule, cusps of upper and lower cheek teeth extremely high and pointed.

Discussion.—*Arretotherium* Douglass (1901) is the only North American genus of anthracotheres that is characterized by the loss of the protoconule. This genus is confined to the early and middle Miocene and is no doubt, derived from the earlier Oligocene genus *Elomeryx*.

The type of the type species was collected in early Miocene beds along Blacktail Deer Creek in western Montana. It was the first record of a New World Miocene anthracothere, and also the first indication that cusp reduction through the loss of the protoconule was taking place in the New World forms, which in this way parallels some of the Old World genera.

The type of *A. acridens*, the type species, gave little indication of the origin of the genus. The molars could have been derived from either *Elomeryx* or *Aepinacodon*. The P^3 does suggest *Elomeryx* as it does not have the lingual cusp that is found in *Aepinacodon*, but rather the broad posterior internal basin of *Elomeryx*. The first two premolars are greatly reduced, but their position with regard to each other and the canine is purely conjectural.

A second species, *A. fricki* Macdonald & Schultz (1956), from Nebraska has been described recently. This species, based on a badly crushed cranium, also suggests descent from *Elomeryx* through the similarity of the P^3, the unreduced P^{1-2}, and the short diastema between P^1 and the canine. Unfortunately, the posterior nares is de-

stroyed in this specimen so that a comparison with the choanae of these two genera cannot be made.

Another species from the upper Rosebud Flint Hill fauna of South Dakota is being described by Stirton and Gregory. This form also points to *Elomeryx* as a logical ancestor (Stirton, personal communication).

ARRETOTHERIUM ACRIDENS Douglass
Text-fig. 13

Arretotherium acridens Douglass. DOUGLASS, 1901, Am. Philos. Soc., Trans., vol. 20, p. 243, 269, pl. IX, fig. 1–3. MATTHEW, 1909, U. S. Geol. Survey, Bull., 361, p. 109.

Type.—Two fragmentary maxillae, with M^{1-3}, and isolated I^3, C, P^{1-4}. CM 704.

Type locality.—Blacktail Deer Creek beds, 30 miles SE of Dillon, Montana.

Horizon.—Blacktail Deer Creek beds.

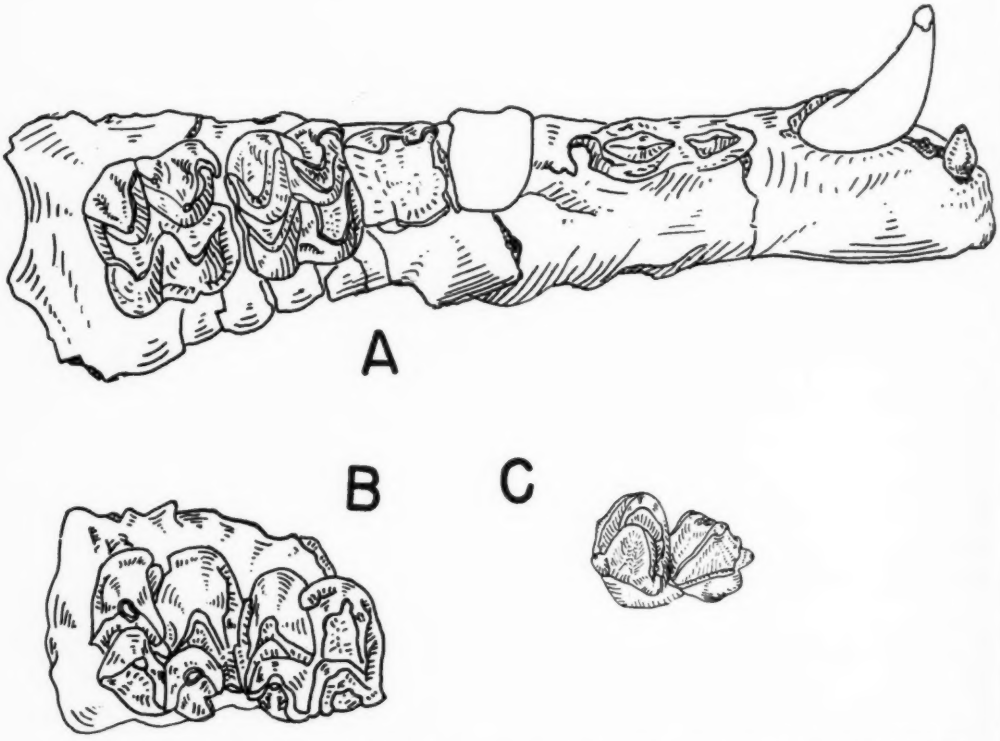
Age.—Arikareean.

Type figure.—Douglass, 1901, pl. IX, fig. 1–3.

Diagnosis.—Canine laterally compressed, upper premolars reduced, P with protocene not connected labially to cingulum, upper molars massive with heavy cinguli.

Discussion.—For many years the type of this species was the only known Miocene anthracothere specimen from the New World. It represented a parallel development between the Old and the New World forms in the reduction of the protoconule.

Douglass' figures, (1901, pl. IX, fig. 1,2) show a reconstruction of the maxillary anterior of the M^1 with P^{3-4} modeled from the left side. Douglass stated that this reconstruction was conjectural due to the fragmentary nature of the type. He indicates a short rostrum as in *Elomeryx*, which at that time was not defensible; but with additional material we now know that this probably is correct.



TEXT-FIG. 13—*Arretotherium acridens* (type specimen), skull fragments: *A*, I^3, P^{1-2}, M^{1-3}; *B*, M^{1-2}; *C*, P^{3-4}. *CM* 704. $\times\frac{2}{3}$.

Table of Measurements (mm.)

	Right	Left
I^1 A-P diam.	7.1	
I^1 Tr diam.	3.5	
P^1 A-P diam.	9.1	
P^1 Tr diam.	3.9	
P^4 A-P diam.		15.6
P^4 Tr diam.		19.1
M^1 A-P diam.	18.3	
M^1 Tr diam.	24.8	25.6
M^2 A-P diam.	26.8	26.8
M^2 Tr diam.	28.3	
M^3 A-P diam.	29.6	
M^{1-3} total length	72.5	

ARRETOTHERIUM FRICKI Macdonald & Schultz

Arretotherium fricki Macdonald & Schultz, MACDONALD & SCHULTZ, 1955, p. 53, fig. 1–3.

Type.—A cranium, with alveoli for canines and P^1–M^3. UNSM 5764.

Type locality.—One-half mile SE of USNM Loc. BX-12.

Horizon.—Marsland.

Age.—Hemingfordian

Type figure.—Macdonald & Schultz, 1956, fig. 1–3.

Diagnosis.—M^3 with mesostyle not notched to base by transverse valley, P^4 greatly reduced, P^2 similar to P^3, P^{1-3} unreduced, Canine with little lateral compression.

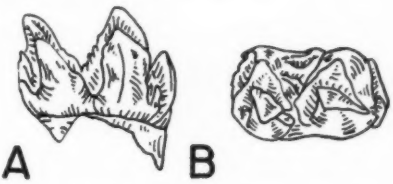
Discussion.—This species strongly suggests the ancestral relationship of *Elomeryx* to *Arretotherium*. Although the choanal region of the type's palate is badly broken so that this characteristic feature of *Elomeryx* cannot be found, the relationship is indicated by the short rostrum, the reduced diastema between the canine and P^1, the shape of the P^2 and the general conformation of the top of the cranium. This species may very well be a direct descendant of *A. acridens*.

Table of Measurements (mm.)

	UNSM Left	UNSM Right
M^3 A-P diam.	25.7	
M^3 Tr diam.	24.9	
M^2 A-P diam.	24.4	24.6
M^2 Tr diam.	23.3	24.4
M^1 A-P diam.	19.6	18.7
M^1 Tr diam.	20.7	20.4
P^4 A-P diam.	12.6	
P^4 Tr diam.	15.3	
P^3 length of blade	16.1	
P^3 Tr diam.	12.7	
P^2 Tr diam.	7.9	
P^1 A-P diam.		9.8
P^1 Tr diam.		5.0
Diastema Canine—P^1	15.5	
Canine alveolus A-P diam.	11.1	
Canine alveolus Tr diam.	7.3	
Canine—M^3	142.1	
P^1–M^3	119.5	
M^{1-3}	68.1	

ARRETOTHERIUM sp.
Text-fig. 14

A single ?P_2 (SDSM 53440) from the Hemingfordian Flint Hill quarry near Martin, South Dakota indicates the type of lower molars found in this genus. The metaconid and entoconid sharply triangular, the protoconid and hypoconid are tall, sharp edged and arcuate, with the crests of the ridges slightly serrate due to the heavy wrinkling of the enamel. This tooth does not differ in basic design from that of *Elomeryx* although the details are somewhat modified. The greatest antero-posterior diameter is approximately 20.4 mm. and the greatest transverse diameter is 11.3 mm.



TEXT-FIG. *14*—*Arretotherium* sp., M_1 or M_2: *A*, lateral view; *B*, occlusal view. SDSM 53440. ×1.

Genus KUKUSEPASUTANKA[2]
n. gen.

Type species.—*Kukusepasutanka schultzi*, n. sp.

Range.—Early Miocene, North America.

Diagnosis.—Cranium large, massive with large tubular snout; M^3 with large bulbous stylar cusps, transverse valley wide, deeply invading mesostyle; P^{2-3} with large lingual-posterior heel; P^2 unreduced.

The genus *Kukusepasutanka* is established on the basis of *K. schultzi* which is described below, This form represents a

[2] *Kukuse*—hog, *pasu*—nose, *tanka*—big; i.e., big-nosed-hog in Sioux, an allusion to the great tubular snout of the type species. Orthography courtesy of Mrs. M. L. Cable and Mrs. Lulu Standing Elk.

radical departure from the other genera of North American anthracotheres in size, shape and cranial proportions. The plan of the molars is distinctive in several features and the premolars, while similar to those of *Elomeryx*, show several important differences. This genus is apparently a newcomer to North America, coming from the Old World during early Miocene times.

KUKUSEPASUTANKA SCHULTZI,[3] n. sp.
Text-fig. 15,16

Type.—Partial cranium with P^2—M^3. FAM 49463.

Type locality.—Hellgate River, 3 miles east of Drummond Granite County, Montana.

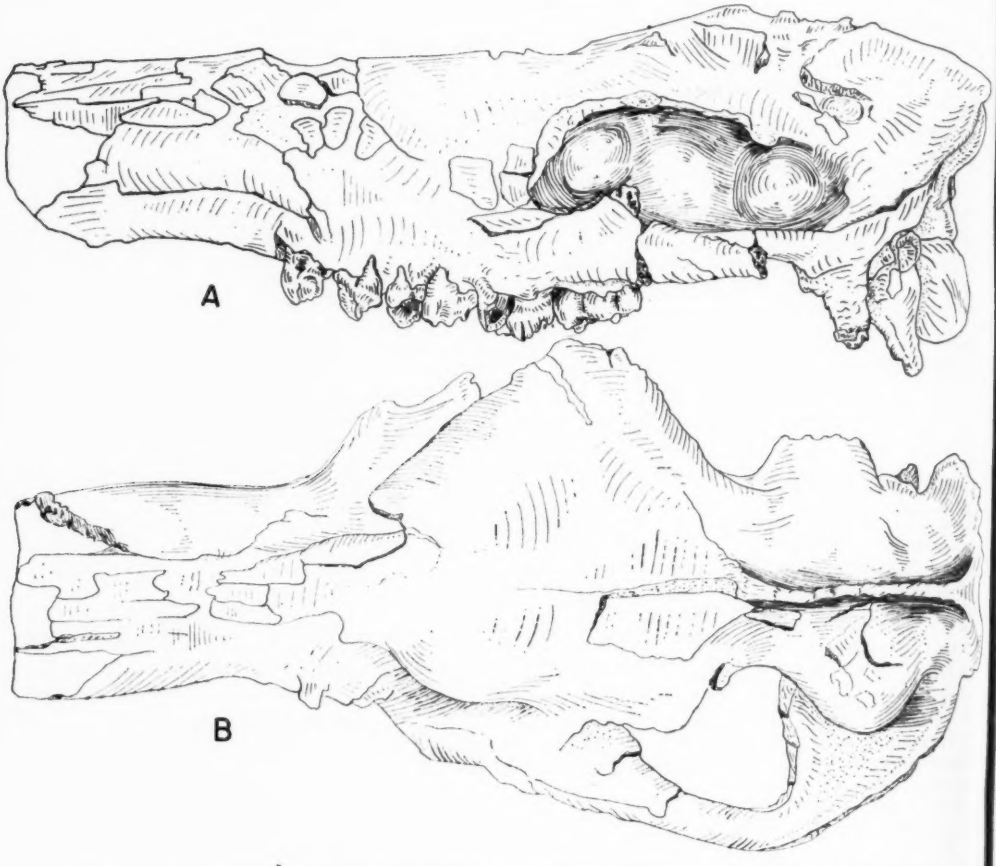
[3] For C. Bertrand Schultz of Lincoln, Nebraska.

Horizon.—"From lower Miocene deposits (approximately equal in age to the Harrison of the Great Plains)." Schultz & Faulkenbach, 1949. p. 124.

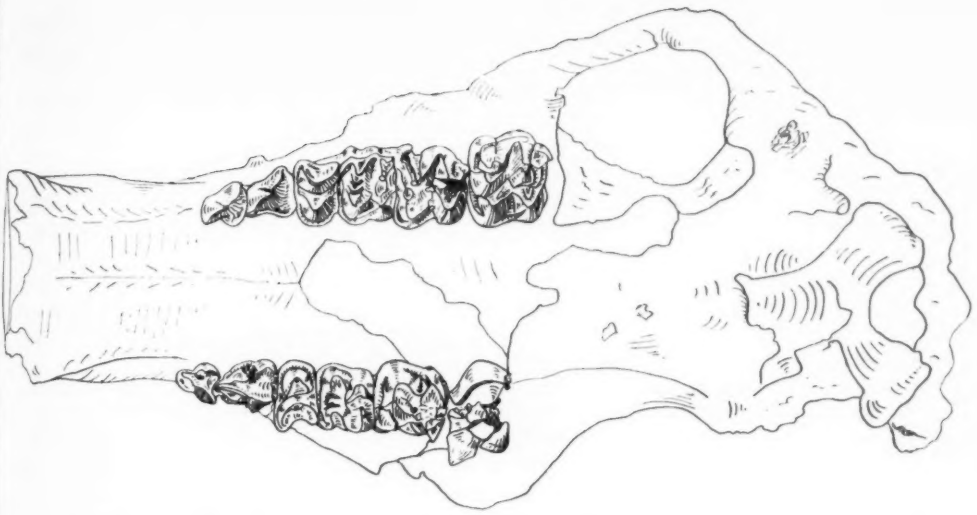
Age.—Arikareean.

Diagnosis.—Cranium large, massive with large tubular snout; M^3 with large bulbous stylar cusps, transverse valley wide, deeply invades mesostyle; P^2 with large internal-posterior heel, similar to P^3; unreduced; P^1 missing.

Description.—M^3 with large bulbous styles similar to *Heptacodon*, mesostyle very broad and deeply invaded by transverse groove which rises with even concave curve to crown, slightly undercutting enamel on anterior edge; paracone and metacone without labial ridge, connected to styles by strong ridges which form deep basins labially to paracone and metacone; protocone, pro-



TEXT-FIG. 15—*Kukusepasutanka schultzi*, n. sp. (type specimen), cranium with P^2–M^3; *A*, lateral view; *B*, dorsal view. F.AM 49463. ×½.



TEXT-FIG. *16*—*Kukusepasutanka schultzi*, n. sp. (type specimen), cranium with P^2–M^3; palatal view. F.AM 49463. ×½.

toconule and hypocone broad and relatively short; transverse valley broadly open and curving posteriorly labially to the metacone. Cingulum interrrupted over lingual side of hypocone and protocone and antero-labial side of parastyle, joined by spur from protoconule opposite the paracone and a spur from the hypocone opposite the metacone, terminates against anterior side of the metastyle. M^2 similar to M^3 with reduced metacone and transverse valley partially blocked by protocone, parastyle broken.

M^1 similar to M^2, cingulum continuous across protocone, parastyle, mesostyle and metastyle greatly reduced.

P^4, labial side deeply basined, paracone deeply basined, protocone conical with weak posterior spur, anterior spur connects to cingulum opposite apex of paracone; cingulum continuous.

Left P^3 conventional *Elomeryx* type with strong transverse blade; the parastyle and the protocone forming the lingual arm and the paracone and the metastyle forming the transverse arm of a right angle triangle, the protocone is very short and connects to the paracone with a flat concave ridge. The right P^3 with parastyle, paracone and metastyle forming an outer pyramidal shaped loop with the long axis closely paralleling the labial edge of the cheek tooth row. Protocone small, on ridge that extends from paracone to lingual edge of tooth just anterior of lingual-posterior corner. Crown forms rough platform anteriorly and lingually of the protoconid ridge resulting in molariformity without molariform cuspation. Cingulum complete, metastyle broken away.

P^2 similar to left P^3, smaller, cingulum reduced.

P^1 lost, with no indication of alveoli.

Canines and incisors missing with anterior portion of rostrum. Cranium badly broken with sutures obscured and choanal region partially destroyed, probably undistorted. Rostrum long and tubular.

Discussion.—The striking feature of the specimen is its massiveness, in contrast to the more delicately streamlined skulls of the various species of *Elomeryx* and *Aepinacodon*. The development of the stylar cusps on the upper molars is more suggestive of *Heptacodon* than either *Elomeryx* or or *Aepinacodon*, but the well developed invasion of the transverse valley into the mesostyle and the long diastemated snout indicates that this form is related more closely to the latter genera.

Species of either *Aepinacodon* or *Elomeryx* could be possible ancestors of this form. Unfortunately, the choanal region of the type has been destroyed so that this structure, which readily differentiates between

Aepinacodon and *Elomeryx*, is not available as a clue to the ancestry of *Kukusepasutanka*.

Certain characteristics are indicative of *Aepinacodon* as a possible ancestor: the elongated snout with the long diastema between P^2 and the canines, the superoccipital region is broad, and the condyles are wide, the lambdoidal crest does not project very far beyond the condyles and joins the zygoma on a broad convex curve. On the other hand, we find an affinity to *Elomeryx* as seen in the similarity of P^2 to the P^3, the gradual flaring of the sagittal crest to the supraorbital process, and the anterior position of the supraorbital process. None of the above may be considered as conclusive, and thus a definite statement of ancestry cannot be made. The most likely origin of this species is from an Old World form and this species is a new immigrant to the New World. In light of the form of the M^3, particularly the stylar cusps, it could have been derived from the European genus *Bothriodon* or an unknown late Oligocene form from either North America or Eurasia.

Table of Measurements (mm.)

	Right	Left
P^2 A-P diam.	19.4	20.0
P^2 Tr diam.	14.0	15.5
P^3 A-P diam.		24.4
P^3 Tr diam.		18.2
P^4 A-P diam.	14.7	15.2
P^4 Tr diam.	24.1	25.3
M^1 A-P diam.	21.7	21.8
M^1 Tr diam.	24.0	23.6
M^2 A-P diam.		29.9
M^2 Tr diam.		33.0 est.
M^3 A-P diam.		34.5
M^3 Tr diam.		37.4
M^{1-3}		85.8

THE ORIGIN OF THE NORTH AMERICAN ANTHRACOTHERES

The appearance without apparent New World ancestors of *Heptacodon* in the earliest Chadronian and of *Aepinacodon* in the late Chadronian strongly suggest that both of these forms were arrivals from the Old World at that time. *Heptacodon* probably arrived during latest Eocene time, as it appears in the earliest Chadronian and *Aepinacodon* at the same time or a little later as our first record is in the late Chadronian Peanut Peak member of the Chadron formation (Clark, 1937, p. 322).[4]

The ancestor of *Heptacodon* is unknown, but as the Anthracotheres are first found in the Middle Eocene of Europe and the Late Eocene of Asia a suitable Old World ancestor surely will come to light in the future.

Aepinacodon is derived easily from the Old World genus *Bothriodon* with which its species have usually been associated. A reduction of the tusks, a shortening of the elongate muzzle, and the reduction of the bulbous stylar cusps would transform the Old World form to the genus found in North America.

Elomeryx is first found in the late Oligocene with the majority of occurrences recorded from the restricted Protoceras channels of the Big Badlands. This form may well be derived from *Aepinacodon* as a continuation of the *Bothriodon-Aepinacodon* line; the transition involving the further shortening of the rostrum, greater reduction of the tusks and an elongation of the palatines into a tubular choanae. As *Elomeryx* is unknown prior to the late Oligocene and *Aepinacodon* is not found after the middle Oligocene, it would seem that one must have replaced the other.

Elomeryx is unknown in the early Miocene of North America but it does occur in the Swiss Aquitanian. Schaub (1948) directed attention to a small species, *Elomeryx minor* (Deperet), which is certainly co-generic with the North American genus and indicates an emigration of this genus to the Old World in late Oligocene or early Miocene times.

Arretotherium, while still not well known, certainly seems to have been derived from *Elomeryx*. The rostrum becomes still shorter, and the protoconule is lost; seemingly, a final step in the *Bothriodon-Aepinacodon-Elomeryx-Arretotherium* sequence. With its apparent extinction in the middle Miocene, the line comes to an end and the native American Anthracotheres disappear from the New World.

Kukusepasutanka, as indicated on a previous page, possibly could have been

[4] Since the manuscript was completed, Morton Green collected a few isolated upper cheek teeth (SDSM 55206) of *Aepinacodon* from the middle Chadronian Crazy Johnson member of the Chadron formation in the Big Badlands.

derived from either *Aepinacodon* or *Elomeryx*, but the massiveness of the cranium, the large tubular snout, the large stylar cusps and the general aspect of the cranium suggests an Old World origin for this genus which is either a new arrival during the early Miocene or an earlier emigrant unknown from the lower horizons.

REFERENCES

CLARK, JOHN, 1937, The stratigraphy and paleontology of the Chadron formation in the Big Badlands of South Dakota: Ann. Carnegie Mus., vol. 25, p. 261–350, 12 fig., 6 pl.

CONNOLLY, J. P., & BUMP, J. D., 1937, Big game hunting in the land of long ago: Nat. Geog. Mag., vol. 91, p. 589–605, illust.

DOUGLASS, EARL, 1901, Fossil Mammalia of the White River Beds of Montana: Am. Philos. Soc., Trans., vol. XX, p. 237–279, 1 map, pl. LX.

GALBREATH, E. C., 1953, A contribution to the Tertiary geology and paleontology of northeastern Colorado: Univ. Kansas Paleont. Contr., vol. 4, p. 1–120, 26 fig., 2 pl.

LAMBE, L. M., 1908, The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan: Contr. Canadian Palaeont., vol. 3, pt. 4, p. 1–65, 13 fig., 8 pl.

LEIDY, JOSEPH, 1856, Notice of some remains of extinct Mammalia, recently discovered by Dr. F. V. Hayden in the bad lands of Nebraska: Acad. Nat. Sci. Philadelphia, Proc., vol. 8, p. 59.

——, 1869, The extinct mammalian fauna of Dakota and Nebraska: Acad. Nat. Sci. Philadelphia, Jour., vol. 7, p. 1–472, 30 pl.

MACDONALD, J. R., 1949, The Pliocene carnivores of the Black Hawk Ranch fauna: Univ. California Pub., Bull. Dept. Geol. Sci., vol. 28, p. 53–80, 15 fig.

——, & SCHULTZ, C. B., 1956, *Arretotherium fricki*, a new Hemingfordian anthracothere from Nebraska: Nebraska State Mus., Bull., vol. XX, p. xxx, 3 fig.

MARSH, O. C., 1890, Notice of new Tertiary Mammals: Am. Jour. Sci., ser. 3, vol. 39, p. 523–525.

——, 1894a, A new Miocene mammal: Am. Jour. Sci., ser. 3, vol. 47, p. 409, 3 fig.

——1894b, Eastern division of the Miohippus beds, with notes on some of the characteristic fossils: Am. Jour. Sci., ser. 3, vol. 48, p. 91–94, 2 fig.

——, 1894c, Miocene artiodactyls from the eastern Miohippus beds: Am. Jour. Sci., ser. 3, vol. 48, p. 175–178, 7 fig.

OSBORN, H. F., & WORTMAN, J. L., 1894, Fossil mammals of the Lower Miocene White River beds: Am. Mus. Nat. Hist., Bull., vol., 6, p. 199–238, 8 fig., pl. 2–3.

SCHAUB, SAMUEL, 1948, *Elomeryx minor* (Depéret), ein bothriodontine aus dem Schweizerischen Aquitainien: Eclog. Geol. Helvetiae, vol. 41, p. 340–347, 3 fig., pl. 13.

SCHULTZ, C. B., & FALKENBACH, C. H., 1949, Promerycochoerinae, a new subfamily of oreodonts: Am. Mus. Nat. Hist., Bull., vol. 93, p. 69–198, 26 fig.

SCOTT, W. B., 1894, The structure and relationships of *Ancodus:* Acad. Nat. Sci. Philadelphia, Jour., vol. 9, p. 461–497, 1 fig., pl. 23–24.

——, *in* Scott, W. B., & Jepsen, G. L., 1940, The mammalian fauna of the White River Oligocene. Part IV. Artiodactyla: Am. Philos. Soc., Trans. vol. 28, p. 363–746, 16 fig., pl. 36–78.

STOCK, CHESTER, 1935, Artiodactyla from the Sespe of the Las Posas Hills, California: Carnegie Inst. Washington, Pub. 453, p. 119–125, 1 pl.

TROXELL, E. L., 1921, The American bothriodonts: Am. Jour. Sci., ser. 5, vol. 1, p. 325–339, 7 fig.

MANUSCRIPT RECEIVED NOVEMBER 15, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3. P. 646–651, 3 TEXT-FIG., MAY 1956

IDENTIFYING FOSSIL AND RECENT BARNACLES BY THE FIGURES IN THE SHELL

IRA E. CORNWALL
1951 Argyle Ave., Victoria, B. C.

ABSTRACT—When shells of sessile barnacles are cut at right angles to the lines of growth, characteristic "figures" can be seen on the polished cut surfaces. The patterns of the figures vary with the species examined, but are constant for each species studied. A number of figures from Recent and fossil species of barnacles are described and illustrated.

IN 1895 Alessandri described "figures" that he observed in thin sections of sessile barnacle shells cut at right angles to the line of growth (Alessandri, 1895). In polished sections examined under low power magnification the figures can be seen between the outer and inner laminae of the shell as lighter areas on the polished surface. In so far as they have been studied and published upon the figures seem to be specifically characteristic of the species of barnacles; but only a limited number of species have been examined. Gruvel (1905, p. 364–371), in his monograph on the Cirripedia shows the figures found in *Chelonobia manati, Coronula, diadema, Cryptotelpas rachianecti, Pachylasma giganteum, Elminius plicatus, Tubicinella trachealis, Xenobalanus globicipitis* and several species of *Balanus*. Madame Claude Davadie-Suaudeau (1952, p. 36–39), shows the figures in *Eliminius plicatus, Pachylasma giganteum, Tetraclita porosa, Balanus concavus, B. tintinnabulum, B. porcatus*, and several others.

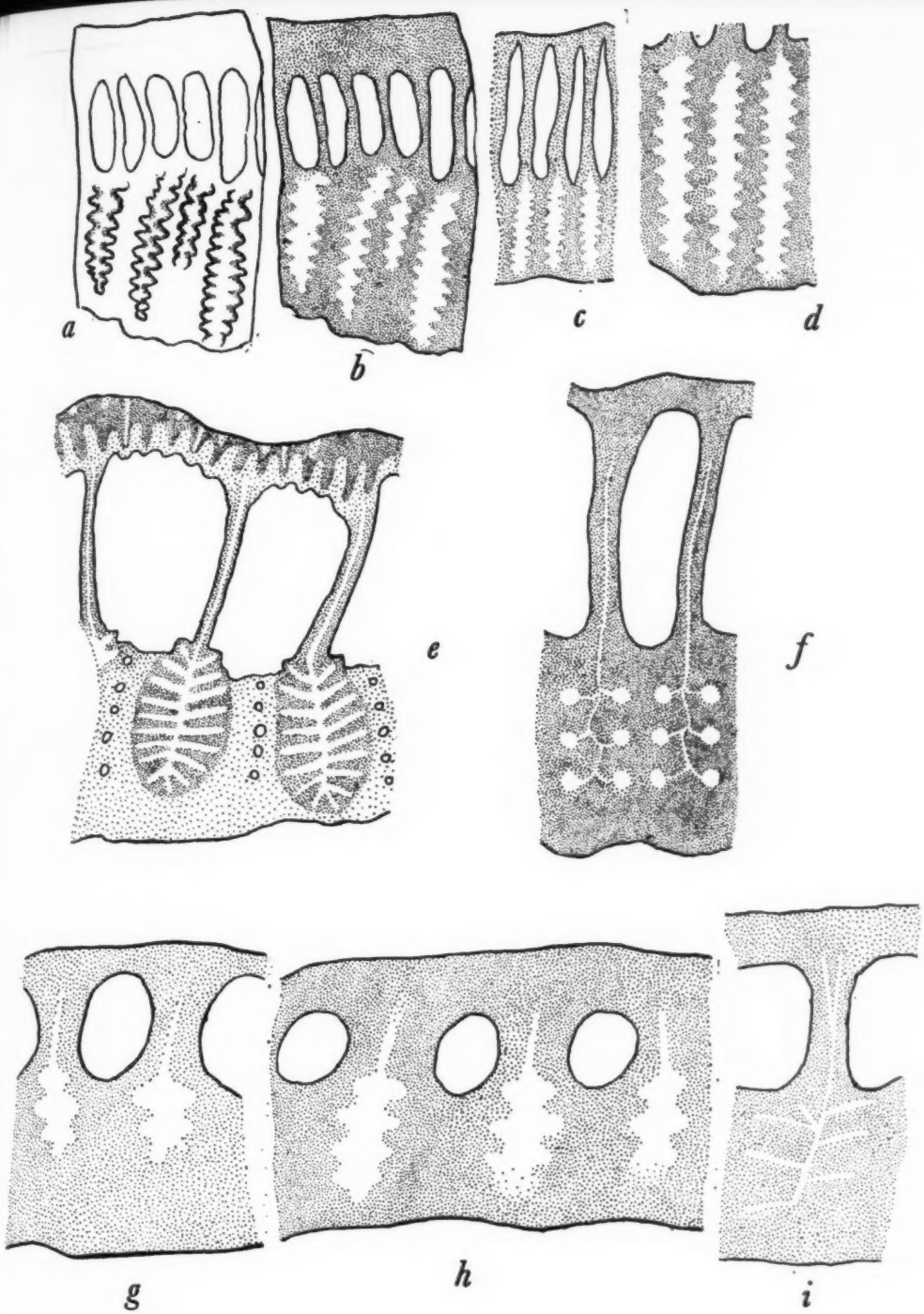
Little use seems to have been made of these figures. In order to take advantage of this character it will be necessary to illustrate a large number of typical figures from many species of Recent and fossil shells. This paper, and the drawings in it, is an attempt to show what can be done if the idea is thoroughly worked out. There is no doubt that the figures can be used for identifying Recent and fossil sessile barnacles, or even fragments of them. Text-fig. 1b shows the figure in *Balanus nubilus*, a common barnacle on the coast at the present time. Text-fig 1d, shows the same figure in a fragment of fossil barnacle shell from the Oligocene Sooke formation, which is referred to later.

Unfortunately the method of identification described can only be used for identifying the shells of sessile barnacles as no figures have been found in the shells of the pedunculate forms.

It has been found that if the shell is cut as recommended and *one* surface polished that the figures can be seen as slightly lighter areas on the polished surface. Many of the figures can be seen even on a dry polished surface, but if they are faint, wetting the surface with water will make them more clearly visible. Dr. J. P. Harding of the British Museum has informed me that the figures are easier to see if the shell is placed in benzyl alcohol after polishing. I have found this method very effective, as it brings out many details that cannot otherwise be seen, unless a thin microscopic section is made.

The figures of Recent barnacles illustrated in this paper are from carefully identified specimens, but I have found a number of figures in unidentified fragments of both Recent and fossil shells which show that there is a great diversity of figures still to be shown. It appears that there are some species that have no figures, but this cannot be definitely stated till many more specimens are examined. Usually the figures are to be found in every wall-plate, and another figure can sometimes be seen if a vertical section is made from the base. The figure in the base is quite different from the figures in the wall-plates.

There are corrugations on the base of the wall-plates that interlock with the corrugations on the edge of the base of the shell. If the corrugations are ground down and the surface polished the figures can be seen. The figures in the base are made visible in



TEXT-FIG. *1*

a–d—*Balanus nubilus* Darwin. *a*, Corrugations on base of wall-plate of specimen from British Columbia coast, ×26; *b*, figures that appear when corrugations are ground down, same specimen, ×26; *c*, figures in wall-plate of specimen from Long Beach, California, ×9.7; *d*, figure in fragment of fossil specimen from Oligocene Sooke formation, Vancouver Island, British Columbia, ×26.

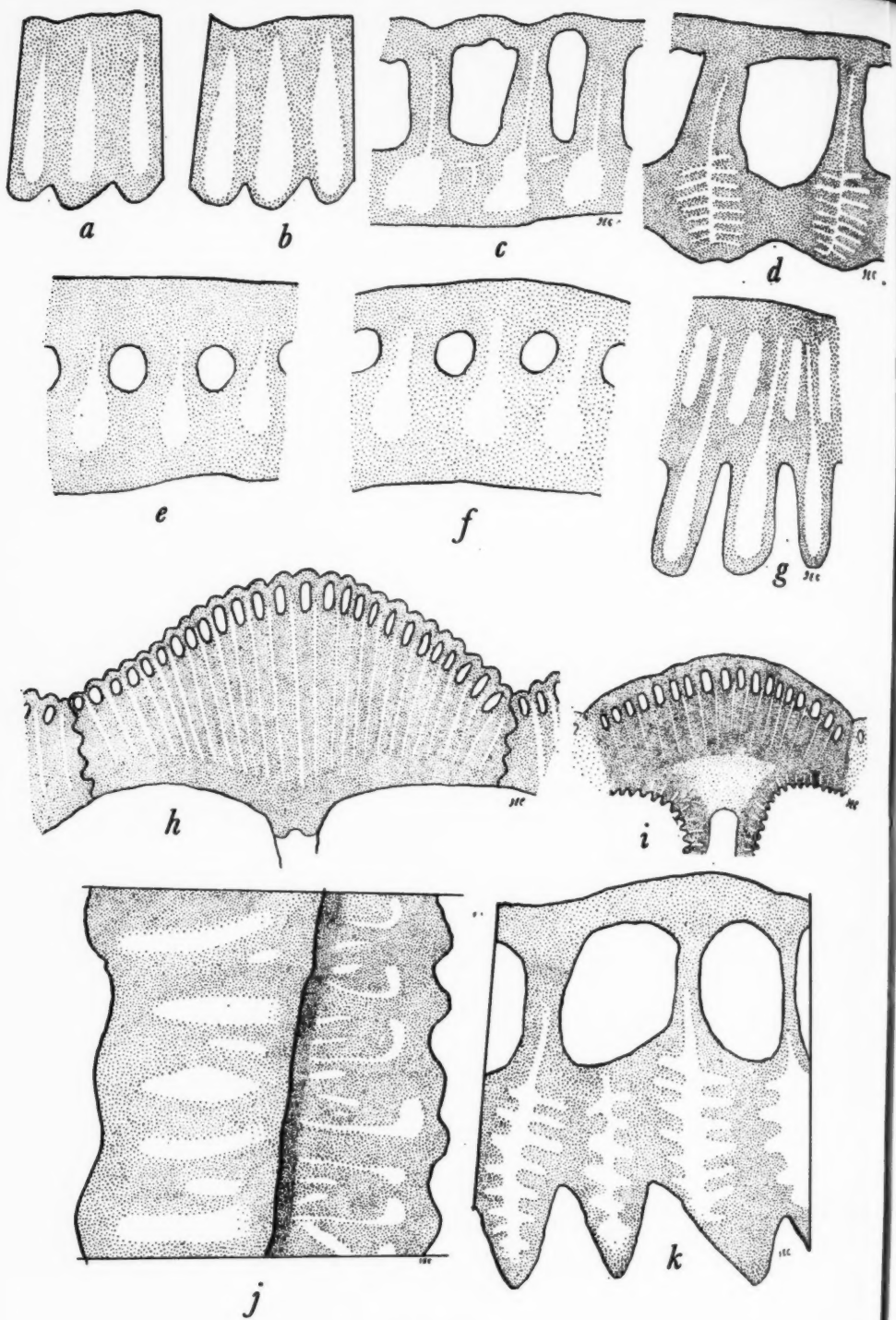
e—*Balanus tintinnabulum californicus* Pilsbry, figures in wall-plates. ×28.

f—*Balanus laevis nitidus* Darwin, USNM 9224, from Peru, figures in wall-plates. ×17.

g—*Balanus concavus pacificus* Pilsbry, USNM 51682, from Long Beach, California, figures in shell of Recent specimen, ×26.

h—*Balanus concavus* Bronn, figures in shell of Miocene specimen from Calvert Beach, Calvert Co., Maryland, ×26.

i—*Balanus amphitrite albicostatus* Pilsbry, USNM 51790 from Japan, figures in shell of Recent specimen, ×26.



TEXT-FIG. 2

a,b—Balanus hesperius f. *laevidomus* Pilsbry, figures in shell, ×32. *a*, USNM 87691, from Hecate Strait, British Columbia; *b*, specimen from Esquimalt Lagoon, Vancouver Island, British Columbia.

c—Balanus crenatus Bruguiere, USNM 11161, from *Albatross* station 2448, Newfoundland. Very faint and irregular figures in shell, ×32.

d—Balanus psittacus (Molina), USNM 89298, from Chile, figures in shell, ×32.

e,f—Balanus improvisus Darwin, figures in shell ×27.3. *e*, USNM 51788 from Chesapeake Beach,

the same way. The figures in the wall-plates resemble the corrugations, and are probably caused by some slight difference in the structure of the shell during the formation of the corrugations. Text-fig. 1a shows the corrugations and Text-fig. 1b shows the figures that are seen when they are ground down. If several sections are made of a wall-plate it will be seen that the figures decrease in size from the base to the apex of the plate.

In making a section of either a Recent or fossil shell for examination it is necessary to see the outer and inner lamina, and a section showing several of the parietal pores. This is necessary because in nearly related species the figures usually are much alike, but there may be a great difference in the shape and arrangment of the pores. The following figures illustrate this point: Text-fig. 2a, *Balanus hesperius*, Text-fig. 2e, *B. improvisus* and Text-fig. 2g, *B. evermanni*, There is a certain resemblance in the figures of these species but the parietal pores are very different. Some species have no parietal pores, while others have several rows of them.

Specimens of the same species from different localities have figures the same, but they may have them arranged in a slightly different manner, as for example the figures in *Balanus nubilus* from the British Columbia coast and the same species from California.

Future investigation will probably show that the resemblance of the figures in different species indicates some relationship between them, but enough work has not been done to be sure this is always the case.

On the south coast of Vancouver Island, British Columbia, and facing the Strait of Juan de Fuca there is an exposure of sandstone, the Sooke formation (Richardson, 1876). It extends for about 70 miles west of Sooke Harbor, and for several miles inland. A quarter of a mile west of Sooke Harbor the sandstone forming the sea cliff has been cut by wave action forming a cliff about 60 feet high; it also forms the beach that is exposed at low tide (Cornwall, 1922).

The small area just west of Sooke Harbor appears to have been formed by a later period of deposition than the sandstone farther west, and its age and stratigraphical position have caused much discussion (Clapp, 1912). Clarke & Arnold (1923) have examined large collections of fossils from this area and have concluded that it is upper Oligocene or lower Miocene in age. It is generally conceded that the Oligocene of this coast is made up of two major periods of deposition, that characterized by *Acilla gettysburgensis* being the upper and that by *Molopophorus lincolnensis* being the lower, and that the area under discussion is part of the *A. gettysburgensis* zone and should be correlated with the Blakeley horizon of Oregon and Washington.

The presence of such genera as *Gonibasis sookensis* Clark & Arnold, *Cyrena sookensis* Clark & Arnold, *Ostrea sookensis* Clark & Arnold, and the extinct sea-cow *Cornwallius sookensis* (Cornwall) indicate that in certain areas there were brackish water conditions, probably near the mouth of a river (Clark & Arnold, 1923).

Many of the fossils found in this formation have analogues living on the coast at the present time and there can be little doubt of their generic relationship (Clark & Arnold 1923, p. 123). A large proportion of the fossil shells are the remains of pelecypods and

---

Maryland; *f*, specimen from Esquimalt Lagoon, Vancouver Island, British Columbia.

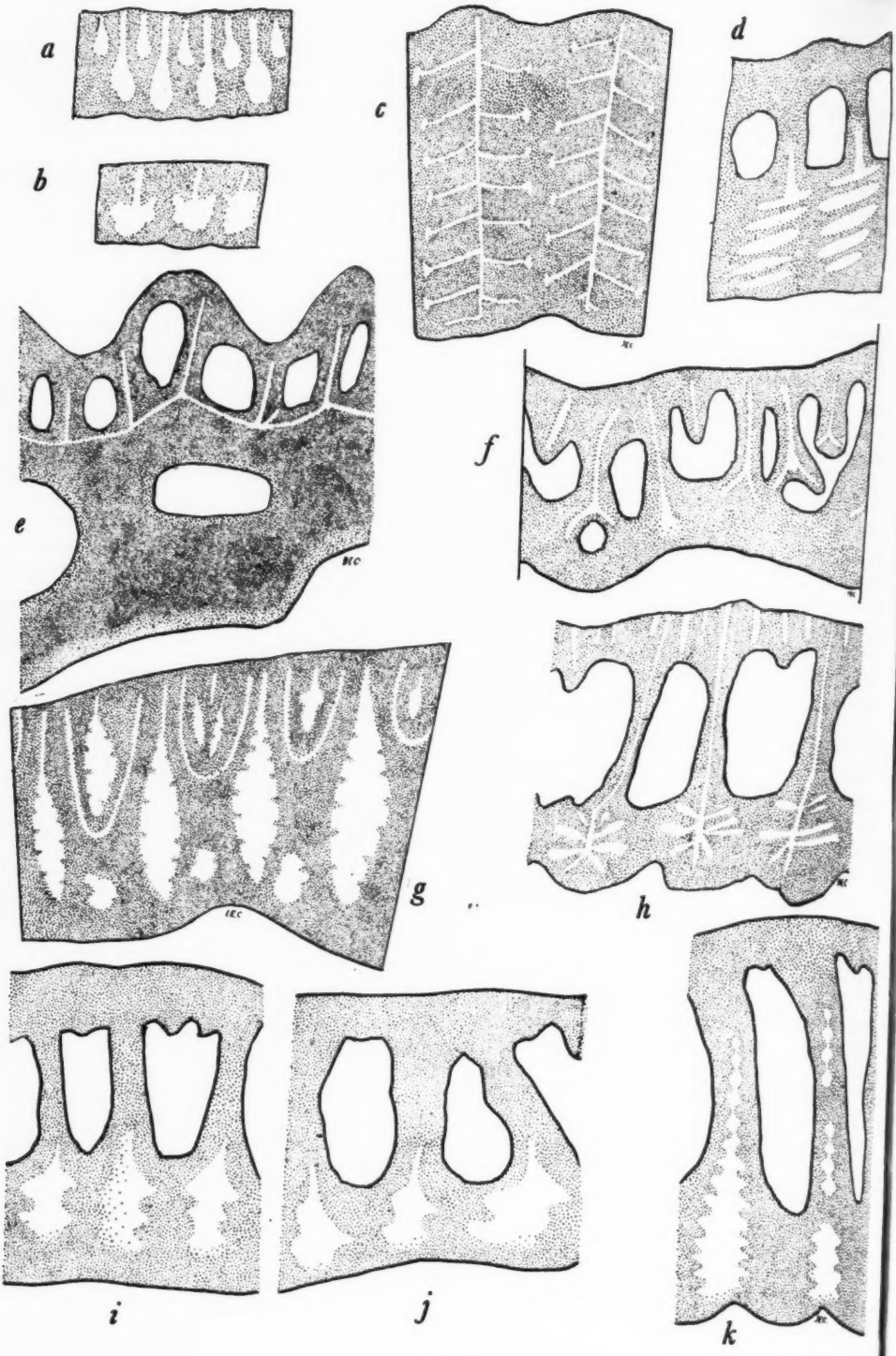
g—*Balanus evermanni* Pilsbry, USNM 53133, from *Albatross* station 3602, Bering Sea, figures in shell, ×11.3. This species has no parietal pores.

h—*Coronula diadema* (Linneaus), from humpback whale (*Megaptera nodosa* (Bonaterre)) at Cachalot Whaling Station, Vancouver Island, British Columbia, figures in one of the T-shaped segments that form the shell, ×16.3.

i—*Coronula reginae* Darwin, from same whale as *h*, figures in one of the T-shaped segments that form the shell, ×28.

j—Fragment from Oligocene Sooke formation, showing sections of two barnacle shells that have grown together, ×21.

k—*Balanus connelli* Cornwall, from Oligocene Sooke formation, ×21. One of the few barnacle shells from the Sooke formation found with the cover-plates in position.



TEXT-FIG. 3

a–d, f,h—Figures in fragments of barnacle shells from Oligocene Sooke formation. *a,b*, ×23; *c*, ×27; *d*, ×23; *f,g*, ×19.2; *h*, ×22.2.

e—Figure in shell of *Balanus* sp. from conglomerate on which Sooke formation rests, ×22.8.

i,j—*Balanus concavus* Bronn, from Miocene Calvert formation, one-half mile north of Scientists' Cliff, Chesapeake Bay, Maryland; figures in different portions of shell, ×27,

k—*Balanus* sp. from Miocene of Pauvrelay, France; figure in carina, ×27.

gastropods; occasionally barnacle shells are found, for the most part broken. One of the complete barnacles found in this formation was described as *Balanus connelli* Cornwall, and the figure found in it is shown in Text-fig. 2k (Cornwall, 1927).

The figures in this paper from Text-fig. 2j to Text-fig. 3h are all figures that have been found in fragments of barnacle shells from the Sooke formation. In all the drawings the top of the figure is the outside of the shell, except in Text-fig. 2j which shows two shells that have grown together. In this case the heavy center line is the outside of the shells.

Text-fig. 3i and 3j show the figures in a very fine specimen of *Balanus concavus* from the Calvert formation that was recently sent to me by the U. S. National Museum. These figures are the same as the figures in Recent *B. concavus* from Long Beach, California. Text-fig. 3k shows the figure in the carina of an unidentified specimen from the Miocene formation of Pauvrelay, France. This specimen was sent to me from the British Museum by Dr. J. P. Harding and it shows very clearly the increase of the size of the figures as the shell grows.

All the drawings in this paper were made by camera lucida directly from the specimens.

ACKNOWLEDGMENTS

The writer would like to take this opportunity of thanking those who have so kindly helped in preparing this paper: Dr. Waldo L. Schmitt and Dr. Fenner A. Chace, Jr., of the U. S. National Museum for many of the specimens shown in the paper, Dr. J. P. Harding of the British Museum for specimens and valuable advice about the method of examining the figures, and Dr. G. Clifford Carl of the British Columbia Provincial Museum for the loan of specimens.

REFERENCES

ALESSANDRI, GIULIO DE, 1895, Contribuzione allo studio dei cirripedi fossili d'Italia: Boll. Soc. Geol. Italiana, vol. 13, fasc. 3, p. 234–314, pl. 3–5.

CLARK, B. L., & ARNOLD, RALPH, 1923, Fauna of the Sooke formation, Vancouver Island, British Columbia: Univ. California Pub., Dept. Geol. Sci. Bull., vol. 14, no. 4, p. 123–234, pl. 15–42.

CLAPP, C. H., 1912, Sooke and Duncan map areas, Vancouver Island, British Columbia: Geol. Survey Canada, Mem. 96, Geol. ser. no. 80, p. 1–445, pl. 1–12.

CORNWALL, I. E., 1922, Some notes on the Sooke formation of southern Vancouver Island, British Columbia: Canadian Field-Naturalist, vol. 36, no. 7, p. 121–123.

——, 1927, Fossil Cirripedia from the upper Oligocene Sooke formation of Vancouver Island, British Columbia: Univ. California Pub., Dept. Geol. Sci. Bull., vol. 16, no. 9, p. 399–408, pl. 58–59.

DAVADIE-SUAUDEAU, (Mme.) CLAUDE, 1952, Contribution a l'étude des Balanidés tertiaires de l'Algérie: Bull. du Service de la Carte Géologique de l'Algérie, ser. 1, Paléontologie, no. 14, p. 1–111, pl. 1–35.

GRUVEL, ABEL, 1905, Monographie des Cirrhipèdes ou Théocostracés: Paris, p. 1–472, fig. 1–427.

RICHARDSON, JAMES, 1876, Report on the coal fields of Nanaimo, Comox, Cowichen, Burrard Inlet and Sooke, British Columbia: Geol. Survey Canada, Rept. Exploration and Surveys, 1876–77, p. 160–192. pl. 8–10, 1 map.

MANUSCRIPT RECEIVED AUGUST 2, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 652–671, 2 TEXT-FIG., MAY 1956

NOTES ON THE NUCINELLIDAE (*PELECYPODA*) WITH DESCRIPTION OF A NEW SPECIES FROM THE EOCENE OF OREGON

H. E. VOKES
The Johns Hopkins University

ABSTRACT—A review of the supraspecific groups of the pelecypod family Nucinellidae shows: (1) that the type of the genus *Nucinella* S. Wood 1861, is *N. miliaris* "Deshayes" Wood (non Deshayes) = *Pleurodon ovalis* Wood from the Pliocene of England; (2) *Pleurodon* Wood 1840, non Harlan 1831, *Nuculina* d'Orbigny 1844, non Porro 1837, *Cyrillona* Iredale 1929, and *Neopleurodon* Hertlein & Strong 1940, are synonyms of *Nucinella;* (3) the name *Huxleyia* Adams, April, 1860, has precedence over *Cyrilla* Adams, June, 1860, since it does not seem to be preoccupied as was thought by Adams; (4) *Cyrillista* Iredale 1929, and *Diabolica* Jousseaume 1897, are synonyms; (5) *Manzanella* Girty 1909, from the Permian is the apparent ancestor of the group, a relationship not previously recognized due to differing accepted orientations of the specimens referred to *Manzanella* and *Nucinella*.

Nucinella oregona, a new species, is described from the upper Eocene of Oregon. An annotated catalogue of the described species shows *Manzanella* to be known from two species, both from the Leonardian Permian of the American southwest; *Nucinella* is known from the lower Jurassic (Hettangian) of Italy, the Cretaceous of southern India, and all epochs of the Tertiary. Eight species are known from the Recent fauna, while four other Recent forms are referred to *Nucinella* (*Huxleyia*).

INTRODUCTION

THE crest and upper slopes of Mount Hebo, a summit in the Coast Range of Oregon that is located in the northwest corner of Yamhill County, is composed of granophyric gabbro, part of a large sill that has intruded the upper Eocene Nestucca formation. While mapping the geology of the Spirit Mountain quadrangle, Baldwin & Roberts (1952) found on these upper slopes on the eastern part of the mountain, a few small blocks of partially baked siltstone that had unusually well-preserved molds of fossils on their surfaces. The material came from a landslide area on the south side of Burnt Ridge; the slightly baked condition locates it as from a horizon close to the intrusion. The blocks were sent to the writer for determination of the fossils, and a faunal list has been published (Baldwin & Roberts, 1952, map locality M-2 [= U. S. Geol. Survey Tertiary locality 17879]).

The fauna consists almost entirely of undescribed species; the most interesting being one referable to *Nucinella*, a genus not previously recognized in the west American marine Tertiary faunas, although known to be present in the Recent fauna off the coast of Mexico under the name *Neopleurodon subdolus* (Strong & Hertlein). It was, therefore, deemed desirable to describe the species and record its occurrence in the Eocene of the eastern Pacific faunas.

Early in the course of the investigation it became evident that there had been no agreement among previous students as to generic nomenclature, that there were complex problems involved in the determination of the genotype of *Nucinella*, and that the literature on the genus was so widely scattered that a preliminary catalogue of known species was desirable. Subsequent investigations have served to indicate that *Huxleyia* Adams has priority over *Cyrilla* Adams, and to show that the Permian genus *Manzanella* Girty is to be considered as almost certainly ancestral to *Nucinella*.

THE GENERA OF THE NUCINELLIDAE

Genus NUCINELLA Wood, 1851

Pleurodon WOOD, 1840, Mag. Nat. Hist., ser. 2, vol. 4, p. 250. Type species, *Pleurodon ovalis* Wood, by monotypy.

not *Pleurodon* HARLAN, 1831, Jour. Acad. Nat. Sci., Philadelphia, vol. 6, p. 284. (Mammalia.)

Nuculina D'ORBIGNY, 1844, Pal. France, Cret. Lamell., p. 161. Type species. *Nucula miliaris* Deshayes, by monotypy.

not *Nuculina* "Filippi" PORRO, 1837, Bibl. Ital., vol. 82, p. 55.

Nucinella WOOD, "1850" [1851], Mon. Crag Mollusca, pt. 2, Bivalves, p. 72.
Cyrillona IREDALE, 1929, Records Australian Mus., vol. 17, p. 160. Type species, *Cyrilla dalli* Hedley, by original designation.
Neopleurodon HERTLEIN & STRONG 1940, Zoologica, vol. 25, p. 419. Type species, *Pleurodon subdolus* Strong & Hertlein, by original designation.

The determination of the type species of *Nucinella* presents a problem in nomenclature that is apparently not covered in the present "Regles" and on which there seems no accord in the practice of modern taxonomists. The matter is being referred to the International Commission on Zoological Nomenclature for solution. To explain this problem and the tentative solution here arrived at, the history of the name and the species concerned is summarized below.

The generic name *Pleurodon* was proposed by S. Wood in 1840 with the sole species being *P. ovalis*, then described. At that time Wood made the following entry in the synonymy of his new form: "*Nucula miliaris* (?) Desh. Coq. Foss. des Env. de Par., pl. 36, fig. 7–9." In the discussion of his species he stated.

> . . . The *Nucula miliaris* of M. Deshayes, if not specifically identical with this shell, must be closely allied to it; . . . I have given as a synonyme the above name of Deshayes, presuming his *Nucula miliaris* may be the same shell, but I am unable to discover the internal pit for the ligament he speaks of, and which his figure so conspicuously displays. The crag specimens have a depression placed externally to the teeth on the shorter side, where I imagine the ligament to have been situated. Deshaye's [sic] figure shows seven teeth, whilst the shells from the crag never display more than six, and seldom more than five.

In 1844 d'Orbigny proposed *Nuculina* for *Nucula miliaris* Deshayes, which was said to be the only known species.

Then in 1851 Wood proposed *Nucinella* with the following generic synonymy:

"*Nucula* (sp.). Deshayes, 1829.
Pleurodon. S. Wood, 1840.
Nuculina. D'Orbigny, 1845, sec Gray."

Unfortunately, Wood did not state that his new generic name was proposed as a substitute name for his earlier *Pleurodon* and for *Nuculina*, although it is almost certain that this is the case. A survey of contemporary literature affords little evidence that would indicate that Wood was aware of the prior use of *Pleurodon* Harlan, as that name seems to have been rather generally overlooked; it seems more probable that he felt that it was invalidated by "Pleurodonta, *Fischer; Beck*, 1837" an entry in Gray's "A List of the Genera of Recent Mollusca, Their Synonyma and Types" (1847, p. 173) a work to which he refers several times in his monograph. However, in the absence of any indication, other than the synonymy, to suggest that *Nucinella* was being proposed as a substitute name, it is not possible to fix the type of *Nucinella* on the basis of the fact that *ovalis* was type of the earliest name, *Pleurodon*. Hence the type species has to be arrived at on the basis of its original publication.

In this original publication only one species was referred to the genus. This was done, however, in the following terms:

1. NUCINELLA MILIARIS, Deshayes. Tab. X, fig. 4a–c.
   NUCULA MILIARIS. *Desh.* Coq. Foss. des Env. de Par., tom. i, p. 225, pl. 36, fig. 7–9, 1829.
   PLEURODON OVALIS. *S. Wood.* Illust. in Mag. Nat. Hist., 2d Series, vol. iv, p. 231, pl. 13, fig. 1, 1840.
   —— MILIARIS. *S. Wood.* Catalogue, 1840.

Spec. Char. Testa minima, subovata, laevigata, polita, tumida; postice subtruncata, antice productiore, rotundato-ovata; dentibus 5–6 magnis, obtusis.

Shell minute, subovate smooth, glossy, and tumid; posterior side short, subtruncate, anterior large, roundly ovate; teeth 5–6, large and obtuse.
Diameter, 1/10 of an inch.
Locality. Paris Basin, Grigon.
Cor. Crag, Ramsholt and Sutton.

This pretty little shell . . . is one of the very few of our Crag Molluscs that dates its existence from the Older Tertiaries, or what is called the Eocene Period; as there is reason to believe the species left in the Paris Basin is the true progenitor of our little shell, . . .

As, however, some differences exist between the Crag Fossil, and what is here considered its specific parent, it may be necessary to give a more detailed description and to point out what, perhaps, might be regarded by some Conchologists as of sufficient importance to keep them distinct.

Our little shell in its outward form, slightly resembles a minute specimen of *Nucula nucleus*, except, that it is more tumid; the anterior side constitutes nearly the whole of the shell, the posterior being cut off by an almost straight line from the umbo to the ventral margin. The hinge is composed of five or occasionally six teeth in the right valve, with six or sometimes

> seven in the left, these are arranged in a slightly curved line extending on both sides of the beak, three on each side; those on the posterior or shorter side are placed rather closer together than those on the anterior one, they are prominent, obtuse, and large compared with the size of the shell; those in the center standing nearly perpendicular to the line of the hinge, while the outer ones on both sides have their widest portion in an opposite direction, all placed, of course, so as one set can be interposed between those of the opposite, when the valves are closed. The lateral tooth of the right valve has a deep depression between it and the margin for the reception of a large tooth of the left valve. In a specimen of the French Eocene Fossil in my own cabinet, the teeth do not appear to be quite so obtuse as in the Crag shell, and the umbo is somewhat sharper and more terminal, with a rather more angular outline, the posterior side is apparently more truncated or straight, while the shell is nearly transparent.

There then follows a considerable discussion in which the author contends that the differences between the Crag and the Eocene forms are only those to be expected as a result of variation under changing conditions with the passage of geological time and

> the differences between the shells of the two periods, which are here considered as identical, is less than is oftentimes presented to us by individuals of the same species in the Crag deposits.

It is obvious from the reference to the number of teeth as "5–6," and the statements that the ligament is external and the shell smooth and glossy, that Wood based his description upon the Crag specimens rather than upon the Paris Basin form whose name he applied to the species.

It is noteworthy that not one of those authors who have considered the genus or the species concerned have accepted Wood's conclusions as to the specific identity of the Eocene and the Pliocene forms. The list includes: Bronn (1854, p. 375), Deshayes (1860, p. 825), Hoernes (1864, p. 300–301), Seguenza (1877, p. 1170), Jeffreys (1879, p. 420), Nyst (1881, p. 170), E. A. Smith (1885, p. 231), Ponzi & Meli (1887, p. 695), von Koenen (1893, p. 70), Dall (1898, p. 597), Lamy (1912, p. 430), Cossmann & Peyrot (1914, p. 127), Glibert (1945, p. 50), and Habe (1951, p. 45). Hertlein & Strong (1940, p. 418–419) do not discuss the matter, but appear likewise to consider that the two forms are not conspecific since they suggest that the Pliocene *ovalis* is to be referred to *Neopleurodon* which they propose as a subgenus of *Cyrilla*, at the same time stating that the Eocene *miliaris* is the type of *Nucinella*.

In view of the fact that Wood accepted only one species as referable to his genus, many taxonomists, including the writer, consider that *Nucinella* is a monotypic genus. Since however, he included in the synonymy of the sole accepted species the name *Pleurodon ovalis* Wood, 1840, other taxonomists maintain that *Nucinella* cannot be considered as being monotypic since more than one taxonomic entity was mentioned by name in the original description. Under this point of view the type has to be fixed by subsequent designation. It must be admitted that this latter view gains added support under the action of the Paris Congress in specifically mentioning that species included in a synonymy are available for subsequent desigation as type species (see Bull. Zool. Nomen., vol. 4, 1950, p. 179–80).

In this second view be accepted, the first valid type designation is that of Stoliczka (1871, p. 334) who states: "type, *N. ovalis*, Wood, from miocene beds of the Vienna basin, and from the crag beds of England." Deshayes (1860, p. 824) in discussing *N. miliaris* referred to it as "our little species that has come to be considered as the type of the genus," but this cannot be construed to represent an unequivocal designation.

If the genus be accepted as monotypic, then the type species is either *miliaris* (Deshayes), or, more properly, the form that Wood described and denominated as *miliaris*, and which is today unanimously known under the name *ovalis*. Under the ruling given in Opinion 168 of the International Commission of Zoological Nomenclature cases under which it is clear that the author of a genus based that genus upon certain specimens, rather than upon the broad concept of the species concerned, may be referred to the Commission for a ruling as to the type. More recently, however, at the Copenhagen meeting of the Commission a decision was taken concerning cases where the type species is determined by subsequent designation that embodies a principle which seems equally applicable to the pre-

sent case. As stated by Hemming (1953, p. 69) it was decided that

> where the author of a new generic name, without designating a type species for the nominal genus so established, places in it a species under a name which he clearly indicated that he is using in a different sense from that of its original author, and the species so indicated is the first of the included species to be selected as the type species under Rule (g) in Article 30 . . . the species to be accepted as the type species shall be, not the nominal species cited by the author of the generic name but the species which that author clearly indicated was that to which he was referring when he designated the type species of the genus concerned.

Although in the case of the genus *Nucinella* we are dealing with a situation in which the identification of a monotypic rather than a subsequently selected type species is in question, it is evident from Wood's description and discussion that he was placing in it "a species under a name which he clearly indicated that he was using in a different sense from that of its original author." Since that species is the monotype species of the genus, it therefore is the species that should be accepted as the type species of the genus. Under this interpretation, the writer concludes that the type species of the genus *Nucinella* is to be cited as: *Nucula miliaris* "Deshayes" Wood, 1851 (non Deshayes, 1829) = *Pleurodon ovalis* Wood, 1840.

Subgenus HUXLEYIA Adams, 1860

Huxleyia ADAMS, 1860, Ann. & Mag. Nat. Hist., ser. 3, vol. 5, p. 303. Type species, by monotypy, *Huxleyia sulcata* A. Adams.

Cyrilla ADAMS, 1860, Ann. Mag. Nat. Hist., ser. 3, vol. 5, p. 478. (new name for *Huxleyia* Adams.) Type species *H. sulcata* A. Adams.

Diabolica JOUSSEAUME 1897, Le Naturaliste, vol. 11, p. 265. Type species *Diabolica diabolica* Jousseaume.

Cyrillista IREDALE, 1929, Records Australian Mus., vol. 17, p. 160. Type species, by original designation, *Nuculina* (*Cryilla*) *concentrica* Verco.

In the April, 1860, issue of the Annals and Magazine of Natural History (ser. 3, vol. 5, p. 303) A. Adams proposed the generic name *Huxleyia*, the sole species referred to it being *H. sulcata* A. Adams, then described from "16 miles from Mino-Sima, Straits of Korea; dredged from 63 fathoms." In the June number of the same journal he stated (p. 478):

> In a former paper I gave the name *Huxleyia* to a new genus of bivalve Mollusca. Should, however, this name have been already used, which is not improbable, *Cyrilla* might be substituted for it.

Subsequently, in an article entitled "Note sur quelques nouveaux genres de Mollusques du Japon" published in the Journal de Conchyliologie, vol. 16, 1868, Adams stated (p. 42):

> Je l'avais nommé d'abord, d'après le professeur Huxley . . . mais j'ai dû changer ce nom en apprenant, plus tard, que M. Bowerbank l'avait déjà employé précédemment pour un *Spongiaire*.

Unfortunately I have been unable to find any reference to the use of the name *Huxleyia* by Bowerbank. The name does not appear in any of the standard nomenclators, nor in the several works on sponges consulted. Dall (1898, p. 601) simply states "not *Huxleyia* Bowerbank" presumably after Adams since he gives no reference to any such usage. Similar statements are made by Lamy (1912, p. 431), Cossmann & Peyrot (1914, p. 127), and Habe (1951, p. 46). The generic name *Huxleya* proposed in 1858 by Dyster, in Bryozoa, and by Claparede & Lachmann in Protozoa, does not invalidate the use of *Huxleyia*, since, as stated by the International Commission on Zoological Nomenclature, "A generic name is not to be treated as a homonym of another such name if it differs from it in spelling by even one letter" (see Hemming, 1953, p. 78). Hence, since there is no such term as *Huxleyia* Bowerbank published prior to April 1860, the generic name *Huxleyia* A. Adams must be the valid name for the group of species that have generally been referred to *Cyrilla*.

Typical species of *Huxleyia* are characterized by the fact that the ligament is situated on the hinge-plate immediately anterior to the cardinal series; in contrast, the ligament of *Nucinella ovata* is described as external, and is certainly so located in "*Pleurodon*" *subdolus* Strong & Hertlein (1937, p. 162, pl. 35, fig. 14,18,19). On the other hand, as pointed out by Dall (1898, p. 599) this is a variable character, and in some species including *miliaris* (Deshayes) and *sequenzai* (Dall), it is located in a pit that is situated at the extreme outer edge of the hinge-plate. The writer uses the

name *Huxleyia* as a subgenus of *Nucinella* for those species in which the liagment has attained a position on the hingle-plate in line with the cardinal teeth and is located immediately adjacent to the anteriormost teeth of that series. This stage of development has been reached in but four species, all of which are known only from the Recent fauna.

Genus MANZANELLA Girty, 1909

Manzanella GIRTY, 1909, U. S. Geol. Survey, Bull. 389, p. 75–76, pl. 10, fig. 3, 4, 4a. Type species, by monotypy, *Manzanella elliptica* GIRTY.

The genus *Manzanella*, well described by Girty, includes small, antero-posteriorly elongate, elliptical shells with rather inflated subcentral umbones which, as interpreted by Girty, are distinctly prosogyrous. The hinge area consists of a series of small more or less transverse teeth located behind the umbos in Girty's orientation of his specimens, with one or two strong lamellar anterior teeth located on a thickened valve margin and supporting internal buttress. Girty thought that he could observe traces of an indistinct ligamental area behind the umbones and above the transverse teeth. Specimens of a second species referred to the genus by Chronic (1952, p. 139, pl. 6, fig. 11a,b, 12–14) from the Kaibab formation of Arizona show a well-developed ligamental area in this position. It was on the basis of the ligament being located behind the umbos, opisthodetic in position, with the beaks distinctly twisted in the opposite side that Girty oriented his specimens with the long lamellar teeth in an anterior position, and the transverse teeth interpreted as lying posterior to them.

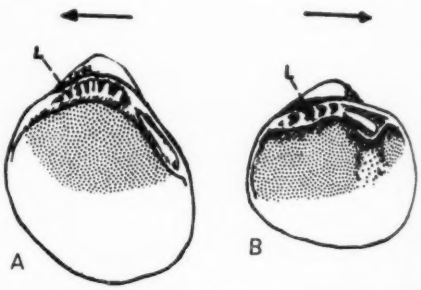
Wood, in describing his "*Pleurodon*" *ovalis* considered that the truncate side of the shell was posterior, apparently by analogy with specimens of *Nucula* as indicated by his discussion in 1851 (see above). This made the long lamellar teeth posterior in position, with the ligament anterior to the umbos, which in *Nucinella* are direct, rather than twisted.

The factors behind these preferred orientations seem to have been overlooked by subsequent authors, and the possible relationship of *Manzanelld* to the Nucinellidae has, as a result, escaped notice. In fact Chronic (1952, p. 139) referring the genus to the family Manzanellidae (presumably a new family in this work) states:

> The taxonomic position of the genus *Manzanella* is very incertain. . . . There is some resemblance to the family Nuculinidae [=Nucinellidae], but in that family as in the genus *Nuculina* [=*Nucinella*], the large lamellar tooth appears to be posterior, the taxodont teeth anterior.

Actually, the relative positions of the ligament, transverse teeth, and the lamellar teeth are identical in the two genera. The evolution of *Nucinella* from *Manzanella* requires only the shortening of the antero-posterior diameter until the valves become slightly higher than long. This will have the effect of "telescoping" the hinge and umbos, bending the hinge-line until the lamellar teeth are located on the lateral margin of the valve, with the umbos, now direct, being situated above the transverse tooth series, and the ligament pushed to a position above the anterior end of that series.

So far as the writer is aware, no studies have been made of the anatomy of any of the Recent species of *Nucinella* or *Huxleyia* and the orientations adopted in the descriptions of the various species is to be considered as purely conventional following that initially used by Wood. There is nothing in the shells themselves to suggest any reason for such a preference (see also Dall, 1898, p. 602). The evidence that led Girty to his orientation of *Manzanella*, i.e., the distinctly twisted umbones, interpreted as



TEXT-FIG. 1—Comparison of preferred orientations of *Nucinella* (A) and *Manzanella* (B). The arrows point in the directions that have been interpreted as anterior in each case; "L" marks the position of the ligament. (drawings differently enlarged)

prosogyrous, with the ligament behind them, interpreted as opisthodetic in position, is one commonly found in the Pelecypoda, and suggests that the presently adopted orientation in *Nucinella* may be incorrect. However, in the catalogue of species presented in this report, no effort is made to revise the descriptions to conform to this orientation.

Nucinella oregona, A NEW SPECIES FROM THE EOCENE OF OREGON

The new species of *Nucinella* found by Baldwin & Roberts is represented on two of the small blocks of siltstone that are approximate counterparts. One has on its surface the mold of the interior of a right valve (the holotype) and the exteriors of two right and two left valves; the other has the interiors of two right and two left valves, the very poorly preserved exterior of the holotype, and, as the valves are not strictly counterparts, an additional exterior of a right valve. Since the blocks measure approximately two and one half by four inches, the species was seemingly abundantly represented in the fauna.

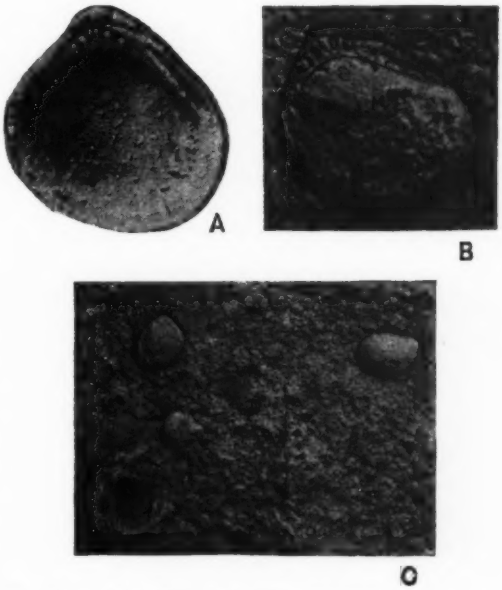
NUCINELLA OREGONA, n. sp.
Text-fig. 2A-2C

Nucinella n. sp., VOKES *in* Baldwin & Roberts, 1952, U. S. Geol. Survey, Oil and Gas Investigations, Map OM 129.

Holotype: USNM 562007; height 3.4 mm, length 3.1 mm, diameter (mold of right valve) ca. 0.75 mm.

The other specimens on the blocks are designated as paratypes (USNM 562008). Their height-length measurements are: left valves, 3.2–2.8 mm.; 3.4–3.0 mm.; right valves 3.3–2.9 mm.; 3.5–3.1 mm. These measurements are made on the molds of the interiors since they show the margins of the valves sharply. It will be noted that a possible pairing of the valves is suggested in which the left valve tends to be slightly smaller than the right. There is, however, no evidence in the position of the valves on the blocks either to confirm or negate this suggestion.

The shell is small, though relatively large for the genus, the average height of 25 previously described species being 2.63 mm. The relatively gigantic "*Pleurodon*" *maximus* Thiele and Jaeckel, which is 12.5 mm. in height was not included in arriving at this average since its dimensions diverge so sharply from those of all other described forms. Including that species the average height is 3.3 mm., approximately that of the present form.



TEXT-FIG. 2—*Nucinella oregona*, n. sp.
A. Latex cast of holotype, a right valve. Length 3.1 mm.; height 3.4 mm. USNM 562007.
B. Natural mold of a left valve, a paratype. Length 2.9 mm., height 3.3 mm. USNM 562008.
C. Latex cast of portion of a block showing holotype in lower left and exteriors of two right valves. (ca. ×3).

The valves are tumid, the degree of inflation being approximately normal for the genus. The umbones are small and direct. The posterior margin is relatively long and slightly convex, almost straight. The anterior margin is also but slightly convex and is approximately three-fourths the length of the posterior. It curves rather sharply into the broadly convex anterior-ventral margin which becomes increasingly more rounded posteriorly, finally sweeping in a broad curve through the posterior-ventral end to join the posterior margin. The surface of the valves is smooth and was apparently polished. There are a few traces of fine growth lines near the ventral margin.

The details of the hinge are exceedingly variable. Of the three right valves, two, including the holotype, have six cardinals, the other has five. The holotype and the specimen with five cardinals show a single rather long lateral tooth on the inner margin of the hinge-plate with a distinct socket between it and the valve margin; the third valve has a strong socket for the reception of the lateral of the opposite valve margined by raised edges that resemble lateral teeth. The raised edge toward the valve margin is relatively short and high, while that toward the inner edge of the hinge-plate is long and lamellar. One of the two left valves has five cardinals, the other, six; both show a lateral socket bounded by raised margins identical with that described above. In the three specimens showing six cardinal teeth, there are two, immediately under the umbo, that are very thin and elongate; the two specimens showing five cardinals have a single tooth in this position that is relatively broad and heavy.

The cardinal teeth are more or less arcuately arranged on the hinge-plate, with the central teeth relatively remote from its inner margin, and the two anterior and two posterior teeth progressively closer to that margin. The terminal teeth of the cardinal series are short and more or less trigonal in shape; the penultimate teeth are stout, moderately long with their upper ends tending to be slightly outwardly curved.

The ligamental area has not been observed and it seems certain that the ligament was external. The anterior adductor scar and the pallial line are also obscured, but the posterior adductor scar, situated immediately below the posterior-ventral end of the hinge-plate is moderately impressed and relatively large.

Only one of the described Eocene species has six teeth in the cardinal series. This is *Nucinella laevigata* (Vincent) (1897, p. xv. text-fig. 3,4) from the upper Eocene "Sables de Wemmel" of Belgium; it differs from *N. oregona* in all details of shape, proportions and hinge structure. The Paleocene *N. ovalina* Cossmann (1887, p. 117, pl. 6, fig. 14,15) is described as having six cardinals, although the original illustrations clearly show eight, and a specimen identified by Vincent (1897, p. xv, text-fig. 2) as this species likewise has eight cardinals. Cossmann's type is a relatively higher shell, the length being but 75% of the height in contrast to the average of 88% in the present species. The posterior lateral tooth is also different, being much shorter and more distant from the cardinal series than is that of those Oregon specimens that show but one lateral tooth.

Nucinella microdus (Boettger) (1869, p. 17, pl. 1, fig. 3a,b) from the middle Oligocene of Germany is described as having five cardinals in the right valve and seven in the left. It may be readily separated from *N. oregona* since it has an ornamentation of slender concentric costae.

Locality.—USGS Tertiary locality 17879. Cut on Hebo Lookout road of U. S. Forest Service, and south side of Burnt Ridge, approximately half way between Cedar Cabin and South Lake. Spirit Mountain Quad., Oregon. Collection E. M. Baldwin & A. E. Roberts, August 23, 1948. Upper Eocene, Nestucca formation.

ANNOTATED CATALOGUE OF DESCRIBED SPECIES, FAMILY NUCINELLIDAE

Permian species

MANZANELLA ELLIPTICA Girty

Manzanella elliptica GIRTY 1909, U. S. Geol. Survey Bull. 389, p. 76, pl. 10, fig. 3,4,4a.

This species, the type of *Manzanella*, was described from the Yeso formation (Leonardian) of New Mexico. Dimensions are not given, but the scale of magnification indicated by Girty for his figures suggests that the largest specimen illustrated has a height of 10 mm. and a length of 12. Under the orientation followed by Girty the hinge consists of four transverse "arched" denticles located posteriorly under the ligamental area and, anterior to the umbos, elongate teeth similar to the "posterior" laterals of *Nucinella*. According to Girty's description there are two such laterals in each valve, the dorsal being supported by the hinge-plate and the ventral resting upon the internal buttress. Chronic, however, states that she has examined Girty's types and that they agree with her Kaibab specimens in this area; these she described (1952, p. 139) as possessing but a single lateral in each valve, both supported by internal buttresses.

The exterior is described as "nearly smooth, marked only by somewhat irregular concentric striae and by occasional inequalities of growth."

MANZANELLA CRYPTODENTATA Chronic

Manzanella cryptodentata CHRONIC 1953, Geol. Soc. Am., Bull., vol. 63, p. 139, pl. 6, fig. 11a, 11b,12,13,14.

This species from the Kaibab formation (Leonardian) of Arizona is described as being similar to *M. elliptica* Girty in all characters except the posterior dentition. This is said to be actinodont, with a low vertical cardinal tooth in the right valve followed by one or more strong, oblique, "posteriorly directed" cardinals behind it. In the only left valve that adequately shows this part of the dentition there is a socket for the right vertical cardinal with a broadly triangular cardinal behind it followed by two narrow obliquely transverse teeth. There is a single anterior lateral in each valve, that of the left valve being received between that of the right and the valve margin. Both are supported by an internal buttress.

The largest specimen for which measurements are given is 9.5 mm. high and 11.4 mm. long.

Jurassic species

NUCINELLA LIASINA (Bistram)

Nuculina liasina BISTRAM 1903, Beiträge zur Kenntnis der Fauna des unteren Lias in der Val Solda, p. 51, pl. 4, fig. 2.

This species is described from the *Psiloceras planorbis* zone of the Hettangian stage, lower Jurassic, near Lake Lugano on the Swiss-Italian border. Dimensions are not given, but the size mark by the illustration indicates a height of 3.15 mm. and a length of 3.0 mm. The figured left valve is obliquely ovate in outline, but judging from the illustrations given by Conti (1954, p. 188, pl. 8, fig. 17–21, text-fig. 48) this feature varies greatly. The type has five transverse teeth in the cardinal series. The lateral plate is relatively short, wholly within the dorsal half of the shell-height, and bears a single lateral on its inner margin. There appears to be, in addition, a shallow socket for a right lateral, or for the raised margin of the lateral socket of the right valve. Exterior smooth.

Cretaceous species

NUCINELLA GLABRATA Stoliczka

Nucinella glabrata STOLICZKA 1871, Mem. Geol. Survey, India, Paleont. Indica, ser. 6, vol. 3, p. 347, pl. 17, fig. 21,21a; pl. 49, fig. 7,8.

This species from the Ootatoor group (Cenomanian ?) at Moraviatoor, southern India is the only Cretaceous form known to the writer. Dimensions are not given, but the original figures (pl. 17) are said to be of four diameters; this indicates a length of approximately 3.1 mm., height 2.4 mm., and a diameter of paired valves of 1.4 mm. The cardinal teeth number six to seven, with one lateral in the right valve and two in the left "remote from the cardinals." The exterior is smooth.

Paleocene species

NUCINELLA OVALINA Cossmann

Nucinella ovalina COSSMANN, 1887, Catal. Illustr. Coq. Foss., l'Eocene Env. Paris, Fasc. 2 (Ann. Soc. Roy. Malac. Belg., vol. 22) p. 117, pl. 6, fig. 14,15.

This species was based on a single right valve collected from the upper Paleocene (Thanetian) at Jonchery, in the Paris Basin, France. The shell is 2.0 mm. high and 1.5 mm. long. It is described as possessing six unequal radiating cardinal teeth; in the original illustration eight somewhat chevron-shaped teeth are apparent. There is a single moderately elongate posterior lateral. The exterior is smooth. The species has been figured by Cossmann & Pissarro (1906, pl. 33, 34, sp. 106-2).

Vincent (1897, p. xv, text-fig. 2) identifies and figures a specimen from the "Landenian" of Belgium as this species. It has eight cardinals, six being relatively large and arranged in a transverse row under the umbo, and two at the posterior end of the series that are smaller and situated on the angulation of the hinge-plate at the posterior-dorsal corner of the valve. The four posterior cardinals are chevron-shaped; the four anterior ones are straight. The specimen, a left valve has a short, but high posterior lateral on the inner margin of the hinge-plate, with an adjacent socket. The shell is said to be 2.5 mm. in height and length.

This Belgian specimen thus differs from the type of *N. ovalina* in shape, proportions, and (apparently) in hinge characteristics.

It may well represent a distinct species. In view of the fact that both forms are known from single specimens that represent opposite valves, and since Cossmann's figure does not agree with his description, it seems undesirable to propose a new name for the Belgian specimen at this time.

NUCINELLA GLABRA (Ravn)

Nuculina glabra RAVN, 1939, Det. Kgl. Danske Vidensk. Selskab., Biol. Skrift., vol. 1, no. 1, p. 30, pl. 1, fig. 3a–c.

The single left valve from the Paleocene at Copenhagen, Denmark, is 1.5 mm. high and 1.4 mm. long. There are four strong cardinal teeth and one posterior lateral on the margin of the hinge-plate with a socket adjacent toward the outer edge of the shell. The shell is a little less oblique than *N. ovalina* Cossmann, the anterior border is straighter, and there are fewer cardinal teeth. The surface is described as having several "stries d'accroissement"; on the illustration these suggest fine concentric sulcations.

Eocene species

NUCINELLA MILIARIS (Deshayes)

Nucula miliaris DESHAYES, 1829, Desc. Coq. Foss. des envir. de Paris, vol. 1, Livr. 15, p. 235, pl. 36, fig. 7,8,9.

According to Cossmann & Pissarro (1906, pl. 33, sp. 106-1) this species is found in the deposits of the Cuisian and Lutetian stages of the Paris Basin Eocene. It is the type species of *Nuculina* d'Orbigny (1844, p. 161), and specimens from the coralline Crag, Pliocene, of England, were misidentified as this species by Wood (1851, p. 73).

In the original publication Deshayes gave the dimensions as "deux millemetres de lon et trois de large," but an examination of his figures suggests that he used a different orientation of his shell from that of later authors. The magnification of his figures 7 and 8, on plate 36, appears to be nine diameters; if this be correct, the dimensions, in accepted orientation, are height 2.5 mm, length 2.4 mm. There are seven to nine cardinals, some are hooked, others straight, and their shape seems to be variable. The figures given by Cossmann & Pissarro suggest that they are more or less radial in position, and that there is a single lateral in the left valve with a socket for its reception in the right. The exterior is marked by distant fine concentric sulcations. Deshayes described the interior as subnacreous, but Wood (1851, p. 74) speaks of the shell as nearly transparent, while Dall (1898, p. 598) states that it is no more nacreous than that of *Leda*.

According to Cossmann (1887, p. 117), Watelet (1870, "Catal. des sables infer." [not seen]) proposed to separate the Cuisian representatives under the name *Nuculina suessoniensis*, but the differences between these and the Lutetian specimens were held to be neither significant nor constant.

NUCINELLA PISSARROI Cossmann

Nucinella pissarroi COSSMANN, 1904, Bull. Soc. des Sci. nat. de l'Ouest de la France, ser. 2, vol. 4, p. 203, pl. 7, fig. 6–9. [Moll. Eoc. de la Loire-Inf., vol. 3, p. 57, pl. 7, fig. 6–9.]

This species from the Lutetian, Eocene, at Bois-Gouët in the Loire basin is externally very similar to *N. miliaris*, but the hinge, as described, is apparently quite distinctive. The original illustrations are not adequate for discriminative study in that area. As described there are five to seven serial teeth immediately under the beaks, that are irregular in shape, and are "reliées le long du bord par des contreforts qui ne sont pas de véritables dents." In each valve there is a large and strong lateral tooth "juxtaposée à une fossette profonde, du côté antérieur; il n'y en a aucune trace du côté posterieur, à la suite des dents seriales, sur de la bord de troncature."

The shell is 3.5 mm. high and 2.5 mm. in length. The exterior is marked by fine concentric sulcations; the illustrations suggest the presence of eight or nine on the larger specimen.

NUCINELLA LAEVIGATA (Vincent)

Nuculina laevigata VINCENT, 1897, Ann. Soc. Roy. Malac. Belg., vol. 32, Bull. des Sceances, An. 1897, p. xv, text-fig. 3,4.

The largest specimen of this species from the "Sables de Wemmel," Auversian, Eocene, of Belgium, is said to be 2.0 mm. high and 1.4 mm. in length. A specimen from Laeken, of these dimensions, has been selected by Glibert (1936, p. 36) as the lectotype; his figure of this form, a right valve

(text-fig. 19), is perhaps the most satisfactory illustration yet presented of a shell of this genus. There are six more or less radiating cardinals in each valve according to Vincent, who describes and figures those of the left valve as being "plus ou moins bifides vers le haut," while those of the right valve are shown (Vincent, fig. 4; Glibert, fig. 19) as irregularly radiating and somewhat chevron-shaped, but without any trace of bifidity. According to Glibert some specimens show seven cardinals. A single strong posterior lateral in the right valve occupies the lower half of the posterior extension of the hinge-plate. The left valve has a small lateral on the inner margin of the plate bordered dorso-laterally by a socket for the reception of the right lateral.

The surface is described as smooth, marked only by faint growth striae. Glibert (1936, p. 37) states however: "La surface, même examinée au microscope, est toujours absolument lisse, seules apparaissent quelques faibles stries concentriques d'accroissement. En outre, chez quelques exemplaires, on distingue des crans de croissance bien marqués."

NUCINELLA OREGONA Vokes

This species is described above from the upper Eocene of Oregon.

Oligocene species

NUCINELLA CINCTA von Koenen

Nucinella cincta VON KOENEN, 1893, Abhand. zur geolog. Specialk. von Preuss u. den Thuringischen Staat., Bd. 10, H. 5, p. 1070, pl. 79, fig. 13a,b,14a,b,15a,b.

This species was described from three somewhat damaged right valves and an immature left valve all collected from the lower Oligocene at Lattorf, north Germany. The left valve measures 2.5 mm. in height and 1.9 in width. Its hinge is immature, and that of the figured right valve is incomplete. The adult hinge is described as consisting of two high teeth before the umbo, three behind it and two slender crowded vertical teeth immediately beneath it. The two anterior and the two most posterior teeth are said to be somewhat oblique in position and shorter than the others. A single posterior lateral is said to occur in the right valve with a socket for its reception in the left. The margins of the socket are somewhat raised, simulating laterals.

It is impossible to reconcile the illustrated hinges with this description. That of the left valve is certainly immature and does not agree in any details. The fragmentary hinge of the only right valve figured (fig. 14b) does not include the anterior end of hinge structure and shows no oblique teeth in this position. The most anterior teeth shown are two slender, apparently broken, teeth immediately under the umbo. Posterior to these are two heavier transverse teeth, and behind them are two short horizontal teeth. In view of the fact that the original description mentions the two anterior teeth as being "high," while the "oblique" teeth are described as "shorter than the others," it seems probable that the hinge includes seven transverse teeth and two "oblique" anterior teeth and two posterior. In this event, the more posterior of the two slender teeth under the umbo in the illustration must be considered as the most anterior of the three teeth described as being behind it; the other slender broken tooth would thus be the posteriormost of the subumbonal pair. If the illustration is accurate, the two posterior teeth that are described as "oblique" are actually sub-horizontal in position.

The surface of the valve is ornamented by numerous fine concentric sulcations.

The author suggests that the form listed by Vincent (1886, p. 13) from the lower Tongrian at Limbourg, Belgium, under the name "*Nucinella ovalis* S. Wood" represents this species.

NUCINELLA MICRODUS (Boettger)

Pleurodon microdus BOETTGER, 1869, Beitr. zur paläont. u. geol. Kenntn. der Tertiär-form. in Hessen, p. 17, pl. 1, fig. 3a,b.

This species was described from strata at Offenbach, Germany, from beds that are, according to von Koenen (1893, p. 1070), of middle Oligocene age. The dimensions of the specimen are not given, but if the original figure is accurate and the scale of magnification exact, the valve is 2.9 mm. high and 2.4 wide. There are said to be seven cardinal teeth in the left and five in the right valve; the illustration suggests that they are somewhat radial in position. A single lateral in the left valve is received in a socket in

the right whose raised margins suggest small parallel lateral teeth. The exterior is described as ornamented by slender concentric costae.

NUCINELLA DOBERGENSIS (Lienenklaus)

Nuculina dobergensis LIENENKLAUS, 1890, Jahresb. naturwiss. Verein zu Osnabrück, vol. 8, p. 121, pl. 2, fig. 4a–c.

This unusually small species from the upper Oligocene "Schichten des Doberges" of the Mainz Tertiary basin was found while searching the marls for foraminifera. A right valve is 1.0 mm. in height and 0.75 mm. wide; all other specimens are said to have comparable dimensions. The hinge is described as consisting of three distant, strong cardinals. There is apparently some variation in the nature of the anterior end of the hinge row which is described as being marked by a groove. The author states that a right and a left valve have this groove smooth; two right valves show a small tooth in this position, while a left valve has two teeth of different length, the longer situated within the groove and extending above close to the shell margin while the shorter is below the groove and near the anterior of the three primary cardinals. There is a single posterior lateral tooth.

Externally the shell is smooth and glossy.

NUCINELLA ZINNDORFI (Zilch)

Pleurodon zinndorfi ZILCH, 1937, Archiv für Molluskenkunde, Bd. 69, H. 5–6, p. 250, text-fig. 1a,b.

This minute species is founded on specimens from the middle Oligocene sand at Welschberg near Waldböckelheim, in the Mainz basin, that were identified by Zinndorf (1928, p. 46) as "*Pleurodon*" *microdus* Boettger. The valve is 1.0 mm. high and 0.8 mm. wide. There are three to four strong cardinals, and in the right valve a relatively short and high posterior lateral. The left hinge is not figured and the posterior lateral area is not described. The exterior is smooth, with fine growth striae.

The species, as pointed out by Zilch, differs markedly in size from *N. microdus*. It needs, however, to be compared with *N. dobergensis* with which it agrees in size and in number of cardinal teeth, and in the right valve, at least in the possession of a single lateral tooth. The difference, if any, may lie in the "groove" in the anterior portion of the hinge area described by Lienenklaus in *N. dobergensis;* no similar structure is mentioned by Zilch.

Miocene species

NUCINELLA CALABRA Seguenza

Nucinella calabra SEGUENZA, 1877, Atti Accad. dei Lincei, anno 274, ser. 3, Mem., vol. 1, p. 1170, pl. 2, fig. 7,7a–d.

The illustrations of this species from the Tortonian, Miocene, Province of Reggio, Italy, differ in almost all significant details from the description. The latter states that the valve is 1.8 mm. high and 1.6 mm. in length, the size mark by the illustration indicates a height of 3.4 mm. The hinge area is described as follows: "Cardo rectus, dentes cardinales 5 irregulares, parum prominentes." As figured the right valve seems to possess two transverse cardinals, with one anterior and one posterior oblique, almost horizontal teeth, while the left valve appears to possess three more or less transverse teeth and a posterior sub-horizontal tooth. The exterior is smooth.

NUCINELLA DUMASI (Cossmann & Peyrot)

Nuculina dumasi COSSMANN & PEYROT 1914, Conch. Neog. Aquitaine, vol. 2, p. 128, pl. 7, fig. 7,8,13,14.

This species is described from a single left valve from the Tortonian, Miocene, at Suabrigues, France. The height is 2.0 mm., and the length 1.75 mm. The hinge plate is short and relatively high, with five almost parallel transverse teeth. The lateral is distant from the cardinals, and is relatively high and short. The exterior is smooth and glossy.

NUCINELLA GUNTERI (Mansfield)

Pleurodon gunteri MANSFIELD, 1932, Florida Geol. Survey Bull. 8, p. 37, pl. 2, fig. 4,6.

A single right valve collected from the "*Arca* zone," late middle Miocene, of the Choctawatchee formation, Florida, is 2.6 mm. in height and 1.8 in length. As illustrated the cardinal area has two transverse teeth with an anterior and a posterior more or less pustular tooth that is sub-horizontal in position. The posterior lateral is long, relatively high, and is situated on the inner

margin of the hinge plate. Exteriorly the shell is smooth except for obscure growth lines.

The details of the hinge agree closely with those figured for the right valve of *N. calabra* Seguenza.

"PLEURODON WOODII Dall" Mansfield

Pleurodon woodii DALL. Mansfield, 1932, Florida Geol. Survey, Bull. 8, p. 37, pl. 2, fig. 1,3.

This species, described by Dall from the Pliocene of Florida, is reported by Mansfield to occur in the upper most Miocene "*Cancellaria* zone" of the Choctawatchee formation, from which a single right valve was collected. This was said to be 2.6 mm. high and 2.0 mm. long. Although Mansfield states: "I see no difference between the Miocene and Pliocene shells" comparison of the illustrations of the two forms suggests that the Miocene one is proportionately shorter, with the posterior lateral slightly more distant from the cardinals, and further, that there are considerable differences in the arrangement of the latter. If the recovery of additional specimens serves to confirm these differences, the separation of the Miocene form as a distinct species will be indicated.

?, NUCINELLA REUSSII Deshayes

Nuculina ovalis (Wood). REUSS, 1860, Sitzungsb. Kais. Akad. Wissensch,. Math.-natur. Kl., (Vienna), Bd. 39, p. 244, pl. 4, fig. 4a,b.
Nucinella reussii DESHAYES, 1860, Descr. anim. sans vert. Bass. Paris, vol. 1, p. 825.
Nucinella ovalis (Wood). HOERNES, 1864, Abh. der K.-K. Reichsanstalt (Vienna), vol. 4, p. 300, 301, pl. 38, fig. 3a–f.

In 1860 Reuss described and figured (1860, p. 244, pl. 4, fig. 4a,b) as *Nuculina ovalis* (Wood) specimens from the Miocene of Bohemia. Later during that year Deshayes stated that Reuss had "considéré comme identique avec celle de Paris, une espèce qui nous paraît différente de la nôtre et de celle du Crag. Nous proposons pour elle le nom de *Nucinella Reussii*." Subsequently, in 1864, Hoernes (1864, p. 300, 301) concluded that the Austrian specimens were to be identified with *N. ovalis*, adding that he could form no conclusion as to their relationships with the French species since no specimens were available to him, but that comparison of original examples convinced him that the Austrian and Crag forms were conspecific. Hoernes figures (pl. 38, fig. 3a–f) a specimen from Forchtenau, Austria, that is said to be 3.0 mm. high and the same in length. The hinge is described as having seven close and irregularly shaped cardinal teeth, and the illustrations show the same number in each valve. The lateral is relatively near the cardinals. The general outline of the valve is very like that shown by Wood for his Crag specimens.

The problem as to the validity of the name *N. reussii* cannot be solved without comparison of specimens in the light of modern interpretations of specific limits. The apparent presence of seven cardinals in each valve in contrast to Wood's description of the Crag specimens as having "five or occasionally six teeth in the right valve, with six or sometimes seven in the left" leads to the presumption that *N. reussii* may prove to be a valid species.

This form is undoubtedly that upon which Stoliczka (1871, p. 334) based his statement that *N. ovalis* was "from miocene beds of the Vienna basin, and from the crag beds of England."

Pliocene species

NUCINELLA OVALIS (Wood)

Pleurodon ovalis WOOD, 1840, Mag. Nat. Hist., ser. 2, vol. 4, p. 230, Suppl. pl. 13, fig. 1.
Nucinella miliaris DESHAYES. Wood, 1851, Mon. Crag. Moll., p. 73, pl. 10, figs. 4a–c.

For description and discussion of this species see that of the genus *Nucinella*, above. Specimens determined as this species have been reported from the following localities and horizons:

1. Lower Tongrian, Oligocene, Belgium (Vincent, 1886, p. 13): see *N. cincta* von Koenen.
2. Miocene, Bohemia (Reuss, 1860, p. 244): see *N. reussii* Deshayes.
3. Miocene, Vienna Basin (Hoernes, 1864, p. 301): see *N. reussii* Deshayes.
4. Miocene, Belgium (Glibert, 1945, p. 50).
5. Pliocene, Belgium (Nyst, 1881, p. 170, pl. 18, fig. 3a–d).
6. Pliocene, Monte Mario, Italy (Cerulli-Irelli, 1907, p. 123): see *N. alibrandi* (Conti).
7. Pliocene (Astian), of Calabria, Italy (Seguenza, 1880, p. 283): see *N. seguenzai* (Dall).

8. Pliocene (Astian) of Calatabria, Sicily (Seguenza, 1877, p. 1170, pl. 2 fig. 8a–c): see discussion under *N. seguenzai* Dall.
9. Recent, Cape of Good Hope, South Africa (Smith, 1885, p. 230): see *N. pretiosa* (Gould).
10. Recent, Straits of Korea (Jeffreys, 1879, p. 123): see *N.* (*Huxleyia*) *sulcata* (A. Adams).

NUCINELLA WOODII (Dall)

Pleurodon woodii DALL, 1898, Trans. Wagner Free Inst. Sci., vol. 3, pt. 4, p. 600, pl. 24, fig. 10.

This species was described from the type area of the Caloosahatchie formation on the Caloosahatchie River in Florida. Dall figures a right valve the dimensions of which are: height, 2.75 mm., length 1.75 mm. The hinge is unusual in that the cardinals occur in two series, an anterior one of three small subparallel teeth trending obliquely forward and downward from a point immediately below the umbone, and a posterior series of three, apparently more or less pustular, transverse teeth, each broader than any of the anterior teeth, and located relatively high on the hinge-plate. There are said to be four cardinals in the posterior series of the left valve. The two series meet at an angle and are separated by a slight gap. The hinge-plate is grooved beneath the posterior series. Externally the shell is smooth, sculptured only by extremely fine incremental lines.

NUCINELLA SEGUENZAI (Dall)

Pleurodon seguenzae DALL,[1] 1898, Trans. Wagner Free Inst. Sci., vol. 3, pt. 4, p. 601.

This species was described as follows:

P. seguenzae Dall, from the Astiano division of the Calabrian Pliocene, was sent to Dr. Jeffreys under the name of *P. ovalis*, and I suppose is the shell so catalogued by Seguenza in his Tert. Fos. of Reggio [1880, p. 283]. It is much larger even than *P. miliaris*, and has the ligamentary fossette somewhat gaping; eight teeth, of which five are posterior, and all are much crowded. The inner edge of the hinge-plate is excavated behind the anterior teeth, and the width of the cardinal border at the lateral teeth is less, proportionately than in the other species.

[1] Since this species was dedicated to Professor G. Seguenza, a man, the specific name is here emended to *seguenzai*.

In a list of dimensions of species (p. 602) Dall indicates for this form: "longest diameter" 5 mm., "antero-posterior diameter" 4 mm. The species has not been figured.

In the paper referred to by Dall, Seguenza gives a reference to an earlier paper in which he had published a figure of a specimen from the "Astiano. Calatabriano" [Sicily] identified as *Nucinella ovalis* (Wood). This figure (Sequenza, 1877, pl. 2, fig. 8a–c) does not agree with Dall's description of his specimen from Calabria. There are five irregular cardinal teeth, and the inner edge of the hinge-plate is straight. The height of the valve is indicated as about 3.6 mm. The exterior is smooth. It seems to be very close to the true *N. ovalis*.

It thus seems probable that there are at least two species represented in the Italian lower Pliocene.

Recent species

NUCINELLA ADAMSI (Dall)

Pleurodon adamsi DALL, 1889, Bull. U. S. Nat. Mus., vol. 37, p. 42. [n.n.].
Pleurodon adamsi DALL, 1898, Trans. Wagner Free Inst. Sci., vol. 3, pt. 4, p. 601, pl. 24, fig. 9.

The type specimen of this species was dredged, apparently from 205 fathoms, 7 miles east of Fowey Rocks, Straits of Florida. Although Dall (1889, p. 42–43) gave the range of the species as from Florida Straits to the Bahamas, and indicated it as being present in East Florida and West Indian waters, the context of his later discussion (1898, p. 598) and description (p. 601) indicate that he had only the right valve originally dredged by Dr. W. H. Rush. The dimensions of this specimen are "longest diameter" 3.25 mm., "antero-posterior diameter" 2.87 mm. The hinge includes three "squarish, high anterior cardinal teeth" arranged in an oblique row, and two "stout conical posterior teeth in the right valve, perhaps three in the other." The inner margin of the socket for the reception of the posterior lateral of the left valve is raised, simulating a tooth, but there is no corresponding swelling on the outer margin of the socket. The exterior is smooth.

NUCINELLA SERREI Lamy

Nucinella serrei LAMY, 1912, Bull. Mus. Nationale d'Hist. Nat., (Paris), vol. 18, no. 7, p. 432, text-fig. 1–3.

A large number of specimens of this species are said to have been recovered from a shell-bearing sand at Bahia, Brazil; no geologic age of the sand is mentioned and it is assumed that this is a recent form. The height is given as 2.5 mm. and the width as 2. mm. The hinge has five unequal cardinals in the left valve and four in the right. There is a relatively small and distant posterior lateral in the left valve, received between paired laterals in the right, these may represent the raised margins of a lateral socket, but are unusually well-developed and hence are interpreted as true lateral teeth. The posterior extension of the hinge-plate is unusually broad, particularly in its more dorsal portion where it extends under the cardinal teeth to a position almost directly beneath the umbo. Lamy's illustrations suggest a slight sinuosity of the pallial line that has not been noted in other species. The exterior is smooth.

NUCINELLA PRETIOSA (Gould)

Nuculina pretiosa GOULD, 1861, Proc. Boston Soc. Nat. Hist., vol. 8, p. 31.

The types of this species were secured by the United States Exploring Expedition from Simon's Bay, off False Bay, Cape of Good Hope South Africa. Smith (1885, p. 230, pl. 19, fig. 1a,b) overlooked Gould's descriptions (1861, p. 31; 1862, p. 170) and gave a full description of the same form, referring it to *Nuculina ovalis* (S. Wood). His specimens were also from Simon's Bay, having been dredged by the *Challenger;* so that Smith's figures represent the first illustrations of this species. Thiele (1934, p. 795, text-fig. 794,a) has also given an excellent figure. The dredgings by the *Valdivia* (Thiele & Jaeckel, 1931, p. 187) extended the known range of the species from Great Fish Bay, southern Angola (16° 26.5′ S; 11° 41.5′ E.) on the North to Algoa Bay (33° 50.5′ S.; 25° 48.8′ E.) on the East.

There appears to be considerable variation in the cardinal area. Gould describes the hinge as having two subapical teeth, two anterior to these and three posteriorly. Smith states that the left valve has seven or eight primary teeth, of which the two anterior and three posterior are somewhat stronger than those intervening. Thiele and Jaeckel note that the cardinals occur in two groups, an anterior group of three strong teeth under the ligament, and a posterior series of six or seven teeth of increasing strength posteriorly. The lateral is described as long and thin. The exterior is smooth, glossy, with a brownish-green periostracum.

NUCINELLA MAXIMA (Thiele & Jaeckel)

Pleurodon maximus THIELE & JAECKEL 1931, Wiss. Ergeb. deutsch. Tiefsee-Exped., *Valdivia*, 1898–1899, Bd. 21, H. 1, p. 188, pl. 1 (6), fig. 28,a,b.

This species, dredged from 254 fathoms in the Zanzibar Channel, East Africa, is by far the largest known in the genus. The height and length are given as 12.5 mm. Only a single left valve is known. The hinge is marked by three strong cardinals ranged obliquely under the ligamental area; behind are two vertical cardinals with what appear to be one or two transverse teeth marking the posterior end of the series. The lateral is long, its inner side marked by an indistinct radial striation. The exterior is smooth.

NUCINELLA HEDLEYI (Cotton & Godfrey)

Pleurodon hedleyi COTTON & GODFREY, 1938, Mollusca of South Australia, pt. I. The Pelecypoda, p. 57. text-fig. 39.

Dredged from 100 fathoms 40 miles south of Cape Wiles, South Australia, the holotype of this species is 4 mm. high and 3.5 mm. long. There are five subequal cardinal teeth arranged in a diverging series; the first and last teeth are short, the others stout and erect. The posterior lateral is long and broad. Exterior is smooth.

NUCINELLA DALLI (Hedley)

Cyrilla dalli HEDLEY, 1902, Mem. Australian Mus., vol. 4, pt. 5, p. 296, text-fig. 44.
Cyrillona dalli (Hedley). IREDALE, 1929, Records Australian Mus., vol. 17, p. 160.

The material on which this species is based was recovered by the *Thetis* in two dredgings off New South Wales, Australia. One was from 41 to 50 fathoms off Cape Three Points, the other from 63 to 75 fathoms off Port Kembla. The species is described as 1.05 mm. in height and 1.2 mm. in length. Examination of the original figure indicates that these dimensions involve the orientation of the shell so that

the umbonal—posteroventral axis is considered as the length; in terms of the more universally accepted orientation of these small shells the valve is higher than long. There are three relatively strong transverse cardinals with a small anterior pustule that is located on the ventral edge of the hinge-plate and a similar, posteriorly located pustule projecting down from the dorsal margin of the plate. The posterior lateral of the left valve is long and strong; it is received in a deep socket in the right valve. The exterior is described as glossy, slightly striated concentrically.

This species is the type of Iredale's (1929, p. 160) *Cyrillona*. The subumbonal ligamental pit, described as a chondrophore, suggests its reference to *Nucinella*, rather than *Cyrilla*.

Nucinella moarianus (Hedley)

Pleurodon moarianus Hedley, 1904, Records Australian Mus., vol. 5, p. 87, text-fig. 14.

Described from two valves dredged in five fathoms off Anchor Island, Dusky Sound, New Zealand, this species is described as being 3.25 mm. high and 2.5 mm. long. There are six cardinals. The first of the anterior series is described as being slender, with the rest erect and stout; as figured, however, the median, subumbonal pair of cardinals are much more weakly developed than the rest. The lateral is broad and long, unique in possessing a subsidiary tubercle on its distal end. The exterior is smooth.

Nucinella subdolus (Strong & Hertlein)

Pleurodon subdolus Strong & Hertlein 1937, Proc. Calif. Acad. Sci., ser. 4, vol. 22, no. 6, p. 162, pl. 35, fig. 14,18,19.
Neopleurodon subdolus (Strong & Hertlein). Hertlein & Strong 1940, Zoologica, vol. 25, pt. 4, p. 419.

This species was described from specimens dredged in 12 fathoms from five miles west of Mazatlan, Sinaloa, Mexico. The holotype, a left valve, is 2.5 mm. high and 1.85 mm. long, a paratype left valve is 2.3 mm. high and 1.65 mm. long, while a right valve is 2.05 mm. high and 1.65 mm. long. According to the original description the cardinal teeth are "small, indistinct, divided into posterior and anterior series, three or four in each, which meet at an angle, those in the posterior series being larger and wider spaced." As illustrated, the left valve has five cardinals, the right, seven; the angle between the two series is not a prominent feature. The hinge-plate is "continued as a shelf along more than half of the the posterior side of each valve, the inner margin turned up and, in the left valve, ending in a lateral tooth." Exterior smooth, white, transluscent.

This species is the type of *Neopleurodon* Hertlein & Strong (1940, p. 419).

A comparison of the respective figures suggests that it was probably this species whose hinge-development was described and figured by Bernard (1898, p. 107–111, pl. 7, fig. 1–7,11). Bernard questionably identified his specimens as *Cyrilla munita* "Carpenter," a name mentioned by Dall, but never described by Carpenter, that was not validated until 1898 by Dall (p. 602). The marginal position of the ligament, even in the adult, and the persistence of the anterior cardinals under the area serve to distinguish Bernard's specimens from both *Huxleyia* and *H. munita*. According to Bernard his specimens were recovered from within a spatangid sent from California by the French consul; if they represent *N. subdolus* they indicate a northward extension of the presently known range of the species.

Nucinella (Huxleyia) sulcata (A. Adams)

Huxleyia sulcata A. Adams, 1860, Ann. Mag. Nat. Hist., ser. 3, vol. 3, p. 303.
Cyrilla sulcata (A. Adams), 1868, Jour. de Conchyl., vol. 16, p. 42, pl. 4, fig. 2,2'.
Nucinella ovalis (Wood). Jefferys, 1879, Linn. Soc. London, Jour., vol. 14, p. 420.
Nucinella ovata Jeffreys. Dunker 1882, Ind. Moll. Mar. Japon, p. 225.

This species, the type of the subgenus, was described by Adams from a specimen dredged in 63 fathoms in the Straits of Korea. In 1868 Adams figured a right valve, the illustration showing six diverging cardinals posterior to a subumbonal ligamental pit that is located in the mid-height of the hinge-plate immediately adjacent to the anteriormost cardinal. There is a single posterior lateral situated above the mid-length of the valve. Dimensions were not given, but the size-mark adjacent of the figures indicates a height of 2.5 mm. and a

length of 2.2 mm. The exterior is very finely and superficially concentrically sulcate. Habe (1953, pl. 29, fig. 10,11) has recently figured a left valve from Moeshima in Kagoshima Bay, Kyushu, Japan, indicating that it is of Pleistocene age. The dimensions are given as height 2.8 mm. and length 2.3 mm. It too has six cardinals and agrees in all details with the figure given by Adams.

In 1879 Jeffreys (1879, p. 420) reported the recovery by Captain St. John, from 40 fathoms off Korea, of a single valve that he identified as *Nucinella ovalis* (Wood), adding:

> I have retained the name "*ovalis*," originally given by Mr. Wood, although it is inappropriate, signifying "belonging to an ovation"; the name ought to be "*ovata*," meaning egg-shaped.

In 1882 Dunker, in his "Index" to the mollusca of Japan, apparently concluding that the Recent Japanese form could not be conspecific with the English Pliocene species, listed a "*Nucinella ovata* Jeffreys." This usage was adopted by subsequent authors, including Pilsbry (1895, p. 150) and Habe (1951, p. 45). Inasmuch as Jeffreys gave not one word of description for his specimen, the name could not possibly have dated from his usage. Furthermore, since he was suggesting that *ovata* "ought" to have been used instead of *ovalis* for the English Pliocene form, it can only be interpreted as an emendation of that name, and hence an unnecessary junior objective synonym of *ovalis*, and not available for the Japanese form.

A single left valve in the Jeffreys collection at the United States National Museum labelled as "Straits of Korea, 40 fathoms, Capt. St. John," is almost certainly the specimen mentioned by Jeffreys. This is identified, apparently in Dall's handwriting, as "*Cyrilla sulcata* A. Adams" and a comparison with the figures of Adams and of Habe leave no doubt as to the correctness of the identification. The hinge shows a relatively large ligamental pit on the hinge-plate with three narrow transverse cardinals immediately behind it and three progressively heavier cardinals posterior to these. There is a long posterior lateral socket with a short high tooth on the inner side of the ventral part of the socket. The valve is somewhat transluscent, with faint concentric external sulcations.

Habe (1953, p. 208) has referred "*Nucinella ovata* Jeffreys" to the synonymy of *N. sulcata* without comment.

NUCINELLA (HUXLEYIA) CONCENTRICA (Verco)

Nuculina (Cyrilla) concentrica VERCO, 1907, Trans. Royal Soc. South Australia, vol. 31, p. 220, pl. 27, fig. 4a,b.
Cyrillista concentrica (Verco). IREDALE, 1929, Records Australian Mus., vol. 17, p. 160.

Cotton & Godfrey (1938, p. 56–57, text-fig. 38) give the range of this species which was described from 104 fathoms 35 miles southwest of Neptune Island, South Australia, as extending from Cape Jaffa to 120 miles west of Eucla, Western Australia, in 17 to 150 fathoms. The holotype is 2.5 mm. in height and 1.9 mm. in length, but Verco notes that a large example is 3 mm. high and 2.3 long. The hinge is marked by a ligamental fossette on the hinge-plate that is anteriorly subumbonal in position. Behind this there are six cardinal teeth, the anterior three being laminar, crowded and vertical in position, the posterior three are progressively more distant, stouter and, being perpendicular to the curving trend of the ventral margin of the hinge-plate, are more diverging in trend. The posterior lateral of the left valve is described as being a "rather long lamellar triangular tooth." The illustration indicates that it has a rather pointed apex at about the mid-height of the valve. The exterior is described as "white, smooth, with six concentric equidistant imbricating steps."

This species, the type of *Cyrillista* Iredale (1929, p. 160) is very close to *Nucinella (Huxleyia) sulcata* (A. Adams).

NUCINELLA (HUXLEYIA) MUNITA Dall

Cyrilla munita Carpenter. DALL, 1898, Trans. Wagner Free Inst. Sci., vol. 3, pt. 4, p. 602.
Nucula petriola DALL, 1916, Proc. U. S. Nat. Mus., vol. 52 (no. 2183), p. 395.

Although Dall several times referred to a "*Cyrilla munita* Carpenter," no such species was ever described by that author, and the first validating description is that given by Dall (1898, p. 602) of a specimen from 30 fathoms off Santa Catalina Island, California. No specimen was figured, and pre-

sumably the specimen whose dimensions were given by Dall as "longest diameter" 2.12 mm., "anteroposterior diameter" 1.75 mm. is to be assumed as representing the type.

In 1916 Dall described (p. 395) but did not figure, a small species that he named *Nucula petriola*. The type of this species has been figured by Schenck (1939, p. 39, pl. 6, fig. 14,15) who states, on the authority of Dr. Harald Rehder of the U. S. National Museum, that it is an undoubted synonym of *munita*. In describing *Nucula petriola* Dall gave the dimensions as 2 mm. in height and 1.25 mm. in length; these cannot be reconciled with those of the type as figured by Schenck. The figures are said to be magnified eight diameters, and indicate a longest diameter of 2 mm. and an anteroposterior diameter of 1.6 mm.; these agree, proportionately, much better with those given by Dall for *munita*.

The rather large ligamental fossette is anteriorly subumbonal in position and is followed, posteriorly, by four transverse and diverging cardinal teeth in the left valve, and five in the right. The anterior pair in the right valve are closely approximate, but the posterior teeth are progressively more distant. There is a single strong posterior lateral tooth in the left valve and a deep, broad socket in the right. The figures given by Schenck suggest that the margins of this socket are slightly raised. The exterior, as described for *Nucula petriola* is smooth and polished, with the prodissoconch visible on the inflated beaks.

The type of *Nucula petriola* was dredged from 53 fathoms off Santa Rosa Island, California. Dall (1921, p. 14) gives the range of *munita* as extending from the Santa Barbara Islands to the Gulf of California, and Keen (1937, pp. 20,23) as from 23° to 37° N. latitude (approximately from Cape San Lucas to the Santa Barbara Islands). Hertlein & Strong (1940, p. 419) state: "Santa Rosa Island, California to ? Lat. 34° S." The basis for the possible southern extension of the range is not known.

NUCINELLA (HUXLEYIA) DIABOLICA (Jousseaume)

Diabolica diabolica JOUSSEAUME, 1897, Le Naturaliste, vol. 11, p. 265.
Nucinella (Cyrilla) diabolica (Jousseaume). LAMY, 1925, Compt. Rend. Congres Soc. Savantes de Paris et des Depts., 1925, p. 503–508; LAMY, 1938, Mem. Inst. Egypt, vol. 37, p. 8, text-fig. 1.

The original description of this species has not been seen; it is reported to have lacked locality reference and illustration. Lamy has figured (1938, p. 8, text-fig. 1) a specimen from the Red Sea, as *Nucinella (Cyrilla) diabolica* that agrees very closely with those of "*Nuculina* sp." given by Bernard (1898, pl. 7, fig. 8,9,13) that also represent specimens from the Red Sea. The specimen figured by Lamy has a height of 2.35 mm. and a length of 1.9 mm.; the corresponding dimensions of an adult valve figured by Bernard (fig. 9) are 2.5 and 2.1 mm., respectively.

The ligamental area of this form is somewhat intermediate between that of typical *Nucinella* and *Huxleyia*. The fossette is on the hinge-plate but is somewhat dorsal in position so that remnants of the anterior cardinal teeth are present on the plate under the fossette. Lamy's figures show four cardinals in the posterior series; the anterior three of these are rather stout and distant, the fourth, pustular in shape. Bernard's figure of the adult hinge shows five cardinals, the first three relatively slender and transverse and progressively more distant posteriorly; the fourth is stout and slightly divergent, while the terminal cardinal is more or less pustular and slightly curved. The posterior lateral of the left valve is located at mid-height, and is rather stout and of moderate length. There is a corresponding groove for its reception on the posterior part of the hinge-plate of the right valve, but the figures do not indicate the presence of lateral teeth or raised margins of the socket. The exterior is smooth; Bernard's figure shows the prodissoconch as visible on the umbo.

Species of Uncertain Validity

NUCINELLA ALIBRANDI (Conti)

Nuculina alibrandi CONTI, 1864, Il Monte Mario ed i suoi fossili subappennini. Ed. 1, p. 23, 47.

According to Ponzi & Meli (1887, p. 672) A. Conti issued, in 1864, a catalogue of the fossils that he had collected from the Pliocene at Monte Mario, near Rome. Subsequently, on the occasion of his presenting the collection to the public museum in

Ferrara, his home city, a second edition (1871), revised and corrected, was published. The present species, described in these catalogues, was referred to *Nucinella ovalis* (Wood) by Ponzi & Meli (1887, p. 695) and Cerulli-Irelli (1907, p. 123; 1909, p. 125, pl. 25, fig. 15). The left valve figured by Cerulli-Irelli seems to have a most unusual arrangement of the cardinal teeth with what appear to be interdigitating elements proceeding from the dorsal and ventral margins of the hinge-plate. This is wholly unlike that of all other species in the genus, including *N. ovalis*, and may well be pathological in nature. Unfortunately, although the specimens in the Conti collection were noted by Cerulli-Irelli he states that he was not able to figure them, and that the illustration given is a specimen in his own collection. Since there is no assurance that the type of Conti's species has a hinge structure identical with that of Cerulli-Irelli's specimen the status of *N. alibrandi* must remain in doubt.

Species Incorrectly Referred to the Nucinellidae

NUCULINA RICCIOLI Conti

Nuculina riccioli CONTI, 1864, Il Monte Mario ed i suoi fossili subappennini. Ed. 1, p. ? [not seen].

According to Cerulli-Irelli (1909, p. 200) examination of the original specimens of this species, founded in the Conti catalogues mentioned above, reveals that it was based upon a pair of broken valves in which the cardinal area is worn and incomplete. It is stated that they do not represent "*Nuculina*," but may be a species of *Nucula*, possibly *N. sulcata* Bronn or *N. placentina* Lamarck.

CYRILLA DECUSSATA A. Adams

Cyrilla decussata A. ADAMS 1862, Ann. Mag. Nat. Hist., ser. 3, vol. 9, p. 295.

Aspalima (*Nipponolimopsis*) *decussata* (A. Adams). HABE, 1953, *in* Kuroda, Ill. cat. Japanese shells, no. 25, p. 206, pl. 29, fig. 20,21.

According to Dall (1988, p. 598) Adams had informed him that this, the second species to be referred to *Cyrilla*, had later proven to be an immature form of a limopsid. This conclusion seems to be borne out by the work of Habe (1953, p. 206) who gives an extended synonymy for the species.

BIBLIOGRAPHY

ADAMS, ARTHUR, 1860, On some new genera and species of Mollusca from Japan: Ann. Mag. Nat. Hist., ser. 3, vol. 5, p. 299–303.

——, 1860a, Mollusca Japonica: New species of *Chrysallida* and *Parthenia:* Ann. Mag. Nat. Hist., ser. 3, vol. 5, p. 477–479.

——, 1862, On some new species of Mollusca from Japan: Ann. Mag. Nat. Hist., ser. 3, vol. 9, p. 295–298.

——, 1868, Note sur quelques nouveaux genres de Mollusques du Japon: Jour. de Conchyl., vol. 16, p. 40–56, pl. 4.

BALDWIN, E. R., & ROBERTS, A. E., 1952, Geology of the Spirit Mountain Quadrangle, Oregon: U. S. Geol. Survey Oil and Gas Investig., Map OM-129.

BERNARD, FELIX, 1898, Recherches ontogéniques et morphologiques sur la coquille des Lamellibranches. Premiere Partie, Taxodontes et Anisomyaires: Ann. Sci. Nat., Zoologique et Paleontologique, vol. 8, p. 1–208, pl. 1–12.

BISTRAM, A., FREIHERR VON, 1903, Beitraege zur Kenntnis der fauna des unteren Lias in der Val Solda: Geolog.-Paleont. Studien in den Comasker Alpen. I; Ber. d. Naturf. Ges. Freiburg i. B., vol. 13, p. 116–208, pl. 1–8.

BOETTGER, OSKAR, 1869, Beitrag zur palaeontologischen und geologischen Kenntniss der Tertiärformation in Hessen: (Inaugural Dissertation), 33 p., 2 pl. Offenbach am Main.

BRONN, H. G., 1853–1856, Lethaea Geognostica, vol. 3, pt. 4, Caeno-Lethaea: T. 6, Mollassen-Periode: 1130 p.

CERULLI-IRELLI, S., 1907, Fauna malacologica marina. Parte prima: Palaeont. Italica, vol. 13, p. 65–139, pl. 3–12.

——, 1909, Fauna malacologica marina. Parte terza e appendice: Palaeont. Italica, vol. 15, p. 125–213, pl. 13–23.

CHRONIC, HALKA, 1952, Molluscan fauna from the Permian Kaibab formation, Walnut Canyon, Arizona: Geol. Soc. Am., Bull., vol. 53, p. 95–166, 11 pl., 15 text-fig.

CONTI, ANGELO, 1864, Il Monte Mario ed i suoi fossili subappennini: 57 p. Ed. 1. Rome. (A second edition was published in 1871 at Ferrara.)

CONTI, SERGIO, 1954, Stratigrafi e paleontologia della Val Solda (Lago di Lugano): Mem. Desc. della Cart Geol. d'Italia, vol. 30, 248 p., 13 pl., 52 text-fig.

COSSMANN, MAURICE, 1897, Catalogue illustre des coquilles fossiles de l'Eocene des environs de Paris: [Duxieme Fascicle], Ann. Soc. Roy. Malac. de Belg., vol. 22, 218 p., 8 pl., text-fig. A–M.

——, 1904, Mollusques Éocéniques de la Loire-inferieure. Pelecypodes, (Parte I): Bull. de la Soc. nat. de l'Ouest de la France, ser. 2, vol. 4, fasc. 3–4, p. 147–213, pl. 1–8.

——, & PISSARRO, GEORGES, 1906, Iconographie compléte des coquilles fossiles de l'Eocene des environs de Paris: Tome 1, pl. 17–38.

——, & PEYROT, A., 1913, Conchologie Neogenique de l'Aquitaine. Tome II, Pelecypodes (Fin et Supplement), Livr. 1: Actes Soc. Linn. Bordeaux, vol. 66, p. 121–324, pl. 1–10.

COTTON, B. C., & GODFREY, F. K., 1938, The mollusks of South Australia. Part I, The Pelecypoda: 314 p., 340 fig., frontispiece. Adelaide.

DALL, W. H., 1898, Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River: Trans. Wagner Free Inst. Sci., vol. 3, pt. 4, p. 571–947, pl. 23–35.

——, 1916, Diagnoses of new species of marine bivalve mollusks from the northwest coast of America in the collection of the United States National Museum: U. S. Nat. Mus., Proc., vol. 52 (no. 2183), p. 393–417.

——, 1921, Summary of the marine shell-bearing mollusks of the northwest coast of America, from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum, with illustrations of hitherto unfigured species: U. S. Nat. Mus., Bull. 112, iii+217 p., 22 pl.

DESHAYES, G. P., 1829, Description des coquilles fossiles des environs de Paris: I. Conchifères: p. 171–242.

——, 1860, Description des animaux sans vertèbres découverts dans le bassin de Paris. I. Mollusques Acéphalés Dimyaires: livr. 19–20, p. 704–912.

DUNKER, GULIELMO, 1882, Index Molluscorum Maris Japonici conscriptue et tablis iconum XVI illustratus: vii+301 p., 16 pl.

GIRTY, G. H., 1909, Paleontology of the Manzano Group: *in* Lee, Willis T., and Girty, George H., The Manzano group of the Rio Grande valley, New Mexico: U. S. Geol. Survey Bull. 389, p. 41–141, pl. 6–12.

GLIBERT, MAXIME, 1936, Faune malacologique des sables de Wemmel, I. Pélécypodes: Mus. Roy d'Hist. Nat. Belg., Mém., 78, 284 p., 7 pl. 75 text-fig.

——, 1945, Faune malacologique du Miocène de la Belgique. I. Pélécypodes: Mus. Roy. d'Hist. Nat. Belg., Mèm., 103, 266 p., 12 pl., 23 text-fig.

GOULD, A. A., 1861, Descriptions of shells collected by the North Pacific Expedition: Boston Soc. Nat. Hist., Proc., vol. 8, p. 14–40.

GRAY, J. E., 1847, A list of the genera of Recent Mollusca, their synonyma and types: Zool. Soc. London, Proc. 1847, p. 128–206.

HABE, TADASHIGE, 1951–1953, Genera of Japanese shells, Pelecypoda and Scaphopoda; No. 1. p. 1–96, text-fig. 1–192 (Feb. 1951); No. 2, p. 97–186, text-fig. 193–478 (Sept. 1951); No. 3, p. 187–279, text-fig. 479–730 (May, 1952); No. 4, p. i–iv, 280–326, text-fig. 731–770 (Jan. 1953).

——, 1953, Limopsidae and Arcidae (1) in Japan: *in* Kuroda, Illustrated Catalogue of Japanese shells: no. 25, p. 201–216, pl. 29,30.

HEDLEY, CHARLES, 1902, Scientific results of the trawling expedition of H.M.C.S. "Thetis." Mollusca, Part I: Brachiopoda and Pelecypoda: Mem. Australian Museum, vol. 4, pt. 5, 38 p., 22 text-fig.

——, 1904, Additions to the marine molluscan fauna of New Zealand: Records Australian Museum, vol. 5, p. 86–97, text-fig. 14–25.

HEMMING, FRANCIS, 1953, Copenhagen decisions on zoological nomenclature; additions to, and modifications of, the Regles Internationales de la Nomenclature Zoologique: xxix+135 p., 2 pl., London.

HERTLEIN, L. G., & STRONG, A. M., 1940, Eastern Pacific expeditions of the New York Zoological Society. XXII. Mollusks from the west coast of Mexico and Central America. Part I: Zoologica, vol. 25, pt. 4, p. 369–430, 2 pl.

HOERNES, MORIZ, 1859–1870, Die fossilen Mollusken des Tertiär-beckens von Wien. II Band: Bivalven: Abh. der K.-K. geol. Reichsanstalt (Vienna), vol. 4, 479, p., 85 pl. [p. 1–116, pl. 1–11, 1859; p. 117–214, pl. 12–31, 1861; p. 215–342, pl. 32–44, 1864; p. 343–430, pl. 45–67, 1867; p. 431–479, pl. 68–85, 1870 (by A. E. Reuss)].

IREDALE, TOM, 1929, Mollusca from the continental shelf of Eastern Australia: Records Australian Mus., vol. 17, p. 157–189, pl. 38–41.

JEFFREYS, J. G., 1879, Notice on some shells dredged by Capt. St. John, R. N., in Korea Strait: Linn. Soc. London, Jour., vol. 14, p. 418–423.

KEEN, A. M., 1937, An abridged check list and bibliography of West North American marine Mollusca: 87 p., 3 fig., Stanford Univ.

KOENEN, A. VON, 1893, Das Norddeutsche Unter-Oligocän und seine Mollusken-fauna. Lief. V: 5. Pelecypoda. I. Asiphonida. A. Monomyaria. B. Heteromyaria. C. Homomyaria. II. Siphonida. A. Integripalliata: König. Preussischen geol. Landes.; Abh. zur geolog. Specialkarte von Preuss., vol. 10, pt. 5, p. 1005–1248, pl. 63–86.

LAMY, ED., 1912, Sur le genre *Pleurodon* ou *Nucinella* S. Wood, avec description d'une espèce nouvelle: Mus. Nat. d'Hist. Naturelle (Paris), Bull., vol. 18, no. 7, p. 429–433, 3 text-fig.

——, 1925, Sur le pretendu genre *Diabolica* Jousseaume (Mollusques Lamellibranches): Compt. Rend., Congres Soc. Savantes de Paris et des Depts., 1925, p. 503–508.

——, 1938, Mollusca testacea: *in* Mission Robert Ph. Dollfus en Egypt: Mem. Inst. Egypt, vol. 37, 88 p., 1 pl. 8 text-fig.

LIENENKLAUS, E., 1890, Die Ober-Oligocän fauna des Doberges: Jahresber. Naturwiss. Verein zu Osnabrück, vol. 8, p. 43–174, 2 pl.

MANSFIELD, W. C., 1932, Miocene pelecypods of the Choctawatchee formation of Florida: Florida State Geol. Survey, Bull. 8, 240 p., 34 pl. 3 text-fig.

NYST, P. H., 1881, Conchyliologie des terrains Tertiaires de la Belgique. Premiere Partie, Terrain Pliocene Scaldesien: Ann. Mus. Roy. d'Hist. Nat. de Belg., ser. Paléont., vol. 3, 263 p., frontispiece and Atlas of 28 pl.

ORBIGNY, A. D. D', 1844, Paléontologie française. Terrains crétacés: vol. 3, (p. 1–807, pl. 237–489 "1843" [1844–1848]). p. 1–288, 1844.

PILSBRY, H. A., 1895, Catalogue of the marine mollusks of Japan, with descriptions of new

species and notes on others collected by Frederick Stearns: viii+196 p., 11 pl. Detroit.

PONZI, S. G., & MELI, R., 1887, Molluschi fossili del Monte Mario presso Roma: Atti dell Accad. dei Lincei, vol. 3, ser. 4, p. 672–698.

RAVN, J. P. J., 1939, Etudes sur les Mollusques du Paléocène de Copenhague: Det. Kgl. Danske Vidensk. Selskab., Biol. Skrift., vol. 1, no. 1, 106 p., 4 pl.

REUSS, A. E., 1860, Die marinen Tertiärschichten Böhmens und ihre Versteinerungen: Sitzungsb. d. kais. Akad. Wissensch., Math-natur. Kl., (Vienna), vol. 39, p. 207–285, 8 pl.

SCHENCK, H. G., 1939, Revised nomenclature for some nuculid pelecypods: Jour. Paleont., vol. 13, p. 21–41, pl. 5–8.

SEGUENZA, G., 1877, Nuculidi terziarie rinvenute nelle provincie meridionali d'Italia: Atti dell' Accad. dei Lincei, Mem., ser. 3, vol. 1, p. 1163–1200, 5 pl.

——, 1880, Le formazioni terziarei nella provincia di Reggio (Calabria): Atti dell' Accad. dei Lincei, Mem. ser. 3, vol. 6, p. 1–446, 17 pl.

SMITH, E. A., 1885, Report on the Lamellibranchiata collected by H. M. S. "Challenger" during the years 1873–76: *in* Voyage of H. M. S. "Challenger," Zoology, vol. 13 (35), p. 1–341, pl. 1–25.

STOLICZKA, FERDINAND, 1870–71, The Cretaceous fauna of southern India. III. The Pelecypoda, with a review of all known genera of this class, fossil and recent: Mem. Geol. Surv. India, Paleont. Indica, ser. 6, vol. 3, p. 1–222, pl. 1–12 (Sept. 1, 1870); p. 223–409, pl. 13–28 (March 1, 1871); p. 410–538, i–xxii, pl. 29–50 (Aug. 1, 1871).

STRONG, A. M., & HERTLEIN, L. G., 1937, The Templeton Crocker expedition of the California Academy of Sciences, 1932, No. 35. New Species of Recent mollusks from the coast of western North America: California Acad. Sci., Proc., ser. 4, vol. 22, no. 6, p. 159–178, pl. 34, 35.

THIELE, JOHANNES, 1934, Handbuch der systematischen weichtierkunde: vol. 3, p. 779–1022, fig. 784–893.

——, & JAECKEL, SIEGFRIED, 1931, Muscheln der deutschen Tiefsee-Expedition: Wissensch. Ergeb. der deutschen Tiefsee-Exped. auf dem Dampfer "Valdivia" 1898–1899, vol. 21, no. 1, p. 159–268, pl. 6–10.

VERCO, JOSEPH C., 1907, Notes on South Australian marine Mollusca, with descriptions of new species.—Part VI: Royal Soc. Australia, Trans. and Proc., vol. 31, p. 213–230, pl. 27,28.

VINCENT, E., 1886, Liste des coquilles du Tongrien inferieur du Limbourg, Belg.: Soc. Roy. Malac. de Belg., Mém., vol. 21, p. 3–16.

——, 1897, Note preliminaire sur *Nuculina*: Soc. Roy. Malac. de Belg., Bull. des Seances, vol. 32, p. xiv–xv, 4 text-figs.

WOOD, SEARLES V., 1840, On the fossil shells of the Crag: Mag. Nat. Hist., vol. 4, p. 230–234.

——, "1850–56" [1851–57], A monograph of the Crag Mollusca with descriptions of shells from the upper Tertiaries of the British Isles. vol. II. Bivalves: London, Palaeontogr. Soc., p. 1–150, pl. 1–12, (June, 1851); p. 151–216, pl. 13–20 (Dec. 1853); p. 217–342, pl. 21–31 (Feb. 1857).

ZILCH, ADOLF, 1937, *Pleurodon zinndorfi*, ein neuer Zweischaler aus dem Tertiär des Mainzer Beckens: Archiv. für Molluskenkunde, vol. 69, no. 5–6, p. 249–251, 3 fig.

ZINNDORF, J., 1928, Der Versteinerungen aus den Tertiär-ablungerungen von Offenbach a. M.-Teil I. Die Conchylien des Ruppeltones (Septarientones): Ber. Offenbacher Verein für Naturkunde, no. 66–68, 65 p., 6 pl.

MANUSCRIPT RECEIVED NOVEMBER 16, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 672–684, 8 TEXT-FIG., MAY 1956

VARIATION AND TOOTH-REPLACEMENT IN A MIOCENE MYLAGAULID RODENT

CRAIG C. BLACK AND ALBERT E. WOOD[1]
Biological Laboratories, Amherst College, Amherst, Massachusetts

ABSTRACT—Serial sections ground from premolars and molars of *Mesogaulus novellus* from Wyoming show great individual and age variation, and demonstrate the difficulty of differentiating species of mylagaulid rodents without serial sections. The problem of tooth homologies is discussed, and it is concluded that the permanent teeth are P_4^4, M_{2-3}^{2-3}, with the deciduous teeth and M_1^1 shed early in life. The type of *M. novellus* is figured and shown to be conspecific with the material from Wyoming, which is of middle Miocene age.

INTRODUCTION

THE Mylagaulidae are a family of peculiar North American middle Tertiary rodents. In at least some individuals, there are paired horns on the nasals, otherwise unknown among the rodents. Whether this is a generic, a specific, or a sexual character is unknown, due to the small number of good skulls available. In addition, the members of the family develop very large and extremely high crowned premolars (P_4^4), which progressively take over more and more of the chewing function, with a concomitant reduction in the importance of the molars.

Good specimens of mylagaulids are rather rare, but isolated premolars are reasonably common in the continental Miocene and Pliocene. However, there is considerable individual and age variation in these teeth, not only in pattern, but also in size and shape, so that it is often difficult or impossible to determine their specific identity.

Very little is known about the changes with wear in the crown pattern in mylagaulids. Determination of such variation should permit the more accurate identification of isolated mylagaulid teeth and might give additional evidence as to the interrelationships of the members of the family. Because of the high crowns of the teeth of these animals, and because of the changes with wear, the only way to be sure of the age-variations that occur is by grinding serial sections. This, of course, results in the destruction of the specimens and hence can only be done where adequate material is available. To date, the only such study was that of McGrew (1941), who sectioned premolars referred to *Mylagaulus monodon* to show the origin and development of the lake pattern from the valleys, and compared them with selected teeth referred to other members of the family. The present paper describes the results of sectioning the teeth of an earlier member of the family, belonging to the genus *Mesogaulus* (*M. novellus*), to show not only age but also individual variation.

About a hundred identifiable isolated teeth from a single middle Miocene locality near Split Rock, seven miles northwest of Muddy Gap, in central Wyoming (five upper premolars, two first upper molars, nine second upper molars, twenty-three third upper molars, nine lower premolars, six first lower molars, sixteen second lower molars, twenty-three third lower molars, one deciduous fourth upper premolar, three deciduous fourth lower premolars and five lower incisors) gave an adequate sampling of the teeth of this form, and permitted a study of age changes as well as individual variation.

SERIAL SECTIONS

Premolars to be ground were embedded in Ward's Bio-Plastic and were ground on a Norton Crystalon wheel. Some of the molars, which are much smaller than the premolars, were embedded in the end of a small cork, and were ground on a small electric hand drill with a grinding wheel attachment, while others were treated in the same way as the premolars. All teeth were

[1] This study was assisted by a grant from the Marsh Fund of the National Academy of Sciences.

ground parallel to the wear surface, and drawings were made at 1 mm. intervals.

Although, in the present study, both the premolars and molars of *M. novellus* were sectioned, the premolars are especially important because most diagnostic and descriptive work on mylagaulids has been based on the pattern of the premolars. Nine teeth were sectioned: two upper and three lower premolars, one upper second molar and three lower second molars. The upper premolars were slightly worn, measuring 7.7 mm. (AC 10310),[2] and 8.2 mm. (AC 10314), from crown to root. Two of the lower premolars were well worn and the third (AC 10308), was nearly unworn, measuring 8.0 mm. from crown to root. All molars were slightly worn.

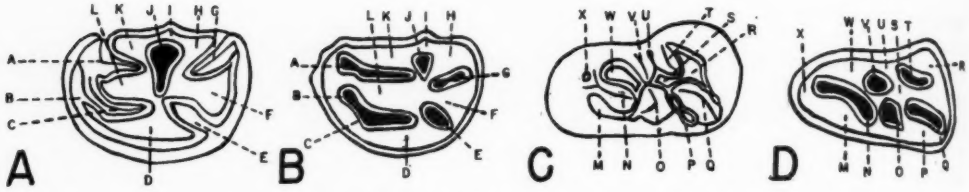
Changes in pattern with wear.—In the development of the high crowns, especially in the premolars, the valleys between the cusps have likewise become deep, and reach through most or all of the crown. This gives a complex enamel pattern throughout the life of the animal, making the tooth persistently effective as a grinding mechanism. In the ancestors of the mylagaulids, the valleys undoubtedly drained to the margin of the tooth. But, with the development of hypsodonty, the outer wall of the tooth was no longer deeply notched by the valleys, presumably an adaptation for strengthening the periphery of the tooth. Therefore, the headwaters or central portions of these valleys are deeper than their mouths. With wear, the valleys are quickly cut off from the outside wall of the tooth, to form lakes (fossettes in the upper teeth and fossettids in the lowers). The walls of the valleys may overhang, resulting in an enlargement of a lake with wear, instead of the more usual decrease in size. Since the valleys are not erosion phenomena, their floors do not have a unidirectional slope, but may be crossed by wrinkles of varying size. These wrinkles may also take part in the increase in crown height of the tooth, in which case wear may result in the separation of a fossette into two parts. Eventually, the wear will reach a level where the enamel at the bottom of the lake is reached, and the lake is transformed into an enamel island. Slight additional wear will eliminate the island completely. Thus, variations in the relative depth of the valleys and in the height of cross-wrinkles can result in variations in the number of lakes, either decreasing or increasing the total. The decrease in number with wear has been generally recognized, but the possibilities of increase have not been so commonly considered. Slight variation in number of lakes, therefore, cannot be considered necessarily to be of taxonomic value.

The drainage pattern of the valleys in the unworn tooth may vary from one individual to another, due to slight differences in the height of the wrinkles between valleys. As a result, a lake may sometimes have one set of connections and sometimes another. These differences in connections between valleys may or may not be taxonomically or phylogenetically significant, but the original relationships of the valleys to the cusps around them are certainly significant. These original relationships are the bases on which names should be given to the valleys and their derivatives. The terminology used in the present paper is indicated in Text-fig. 1, which differs slightly from that of previous authors (as Cook & Gregory, 1941). This terminology, as is true of that of other authors, is an amplification of that proposed by Stirton (1935, p. 392).

Once names have been assigned to valleys, the terminology must be carried through, regardless of what happens with further wear. Thus, in one specimen of *M. novellus*, the protoflexus separates from the paraflexus and gives rise to a protofossette which ultimately divides into two smaller lakes (Text-fig. 2,A–E), whereas in another, the initial division occurs between the two portions of the protofossette, and one remains attached to the paraflexus (and later parafossette) for some time, before becoming separated as a protofossette (Text-fig. 2,G–K). But these differences do not change the homologies of the parts in question and therefore should not require a change in terminology. Similarly, the valley called protofossette by Cook & Gregory (1941, fig. 1) is surely homologous to that given the same name here, even though in our material it is connected with the parafossette and in theirs with the outside margin of the tooth.

In AC 10314 (Text-fig. 2A) the only lake

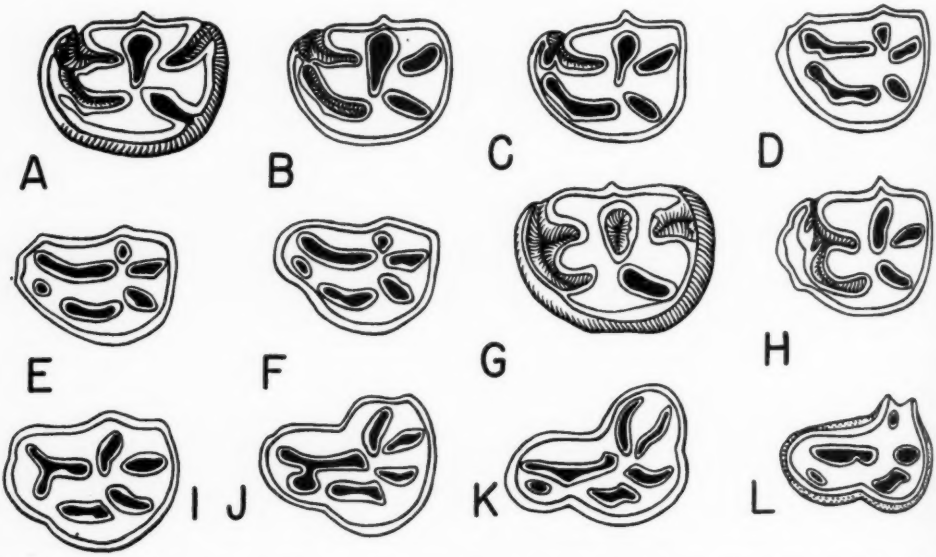
[2] Throughout this paper, AC indicates the Amherst College collection.



TEXT-FIG. *1*—Terminology of parts of mylagaulid teeth, based on premolars of *Mesogaulus novellus*. Anterior ends of all teeth to the left, and buccal sides at the top. A, unworn left P^4; B, worn left P^4; C, unworn right P_4; D, worn right P_4.

Key: A, paraflexus, changing to parafossette; B, anterocone (or anteroloph); C, protoflexus, changing to protofossette; D, protocone (or protocone plus hypocone); E, hypoflexus, changing to hypofossette; F, posteroloph; G, metaflexus, changing to metafossette; H, metacone; I, mesostyle; J, mesoflexus, changing to mesofossette; K, paracone; L, protoconule; M, metaconid; N, anteroflexid, changing to anterofossettid; O, mesoflexid, changing to mesofossettid; P, entoconid; Q, metaflexid, changing to metafossettid; R, hypoconid; S, ectonid; T, hypoflexid, changing to hypofossettid; U, ectostylid; V, protoflexid, changing to protofossettid; W, protoconid; X, anteroconid.

that had formed before the grinding began was the mesofossette. The paraflexus and protoflexus were deep, as was the metaflexus. The hypoflexus was nearly cut off from the outside of the tooth, with only a small valley connecting it with the posterior rim of the tooth. The other upper premolar sectioned (Text-fig. 2G) shows a few differences in pattern. The hypoflexus has already been closed off to form a hypofossette, and the metaflexus opens on the posterior margin of the tooth instead of at the postero-external corner. The paraflexus and protoflexus do not extend as deeply into the interior of tooth as in Text-fig. 2A, the protoflexus being only about half the length in the second tooth that it is in the first. After the removal of one millimeter of the crown, the protofossette has just separated from the paraflexus in one specimen (Text-fig. 2B), while in the other (Text-fig. 2H) the connection between the protoflexus and the paraflexus is as wide as that between the paraflexus and the buccal rim of the tooth. The metafossette and the hypofossette are well defined at this stage in both



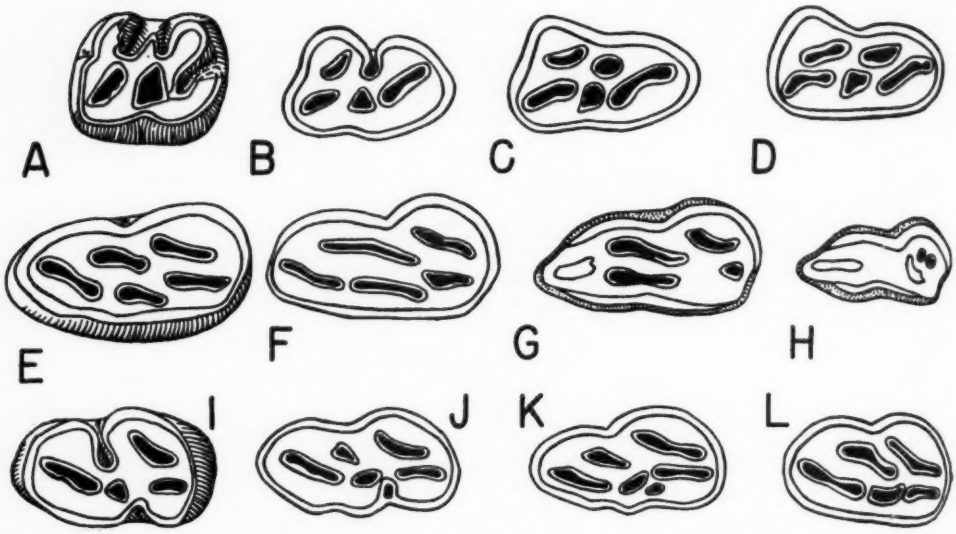
TEXT-FIG. *2*—Serial sections of left upper premolars, *Mesogaulus novellus*, taken at 1 mm. intervals. ×5. A–F, AC 10314; G–L, AC 10310. Note cement around tooth at stage L.

teeth. The differences noted between the two specimens are even more pronounced at the third stage, since the paraflexus has still not been closed off in one specimen (Text-fig. 2C), but in the other (Text-fig. 2I) it is isolated as a parafossette and still retains a connection with part of the protofossette, giving it the Y-pattern characteristic of *Mesogaulus* (Cook & Gregory, 1941 p. 551). In Text-fig. 2C the protofossette is a long slender lake isolated from the parafossette, whereas in Text-fig. 2I it is a short lake in the lingual part of the tooth, its buccal portion being the lingual arm of the Y of the parafossette.

At the stages shown by Text-fig. 2D and 2J, the two teeth have different outlines. In the former the tooth is still basically quadrate, but in the latter the anterior portion is narrow as in the specimen shown by Cook & Gregory (1941, fig. 2). The parafossette has been isolated and the crown pattern consists of five lakes in each tooth. In Text-fig. 2J, however, there is still a Y-shaped parafossette while in Text-fig. 2D it is a long lake with a slight buccad projection at its anterior end. After the removal of four millimeters, the anterior end of the protofossette or the lingual arm of the Y (Text-fig. 2K) has separated to form a small, circular lake, making a total of six lakes in the crown pattern. These secondary lakes, though formed in different manners, are completely homologous. In Text-fig. 2,H–K, the mesofossette and metafossette are transversely elongate lakes while in Text-fig. 2,D–F, they are rather small, the mesofossette being a small oval and the metafossette only a little larger and somewhat longer. In AC 10314, there eventually is a reduction of the transverse diameter at the anterior end (Text-fig. 2,E–F). In the final section of AC 10310 the metafossette has been worn away, and the base of the crown has been reached at the postero-buccal corner, so that the enamel is interrrupted here. The remainder of the tooth is surrounded by a layer of cement.

The differences noted between the corresponding wear stages in Text-fig. 2 show individual variation in the population sampled. The most striking differences occur between stages represented by Text-fig. 2B and H on the one hand and 2D and J on the other. This represents the age span in which most specimens would occur, since further wear would normally occur only in extreme old age, represented by small numbers in the population. Differences in pattern such as illustrated might lead one to feel that different species or even genera were represented. Two other specimens that show this area agree with AC 10314 in not having the Y-pattern. There is no justification, however, for considering that two forms are present, since the size of the specimens, the general shape and the rest of the pattern, including particularly the columnar mesostyle, show them to be basically so similar that there is no alternative but to refer them to the same species. The variation noted is, then, a good example of individual variation within members of the same species, even though it technically crosses the boundary between two genera.

Sections of three lower premolars, the first being relatively unworn, are shown in Text-fig. 3. In Text-fig. 3A, the mesofossettid and metafossettid are closed off with the enamel surrounding the anteroflexid just joining that of the mesofossettid. The hypoflexid and the protoflexid have not yet separated from the outer wall of the tooth, and are deep valleys draining buccad. The next section, Text-fig. 3B, resembles the first section of AC 10306 (Text-fig. 3I), which was more worn when it was embedded. At this stage in both teeth the anterofossettid, mesofossettid, metafossettid and hypofossettid are isolated, whereas the protoflexid is still connected with the outside of the teeth. In Text-fig. 3,J–K, the mesoflexid can be seen giving rise to two mesofossettids, the buccal one being formed first and then the more lingual one, in contrast to the conditions in the other specimens, where only a single mesofossettid occurs. The stage of Text-fig. 3C is at essentially the same stage of wear as the first stage of AC 10311 (Text-fig. 3E), with five well-defined lakes. With wear, the anterior half of each tooth narrows progressively. The grinding was continued until the pulp cavities were exposed (Text-fig. 3, G and H). At the last level almost all trace of lakes has vanished, only a few small round spots of enamel being left. As the crown is worn farther and farther down, cement appears



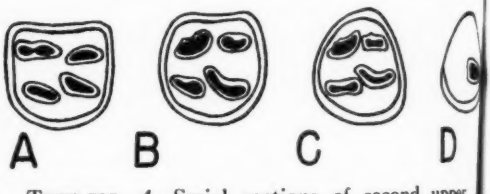
TEXT-FIG. 3—Serial sections of lower premolars, *Mesogaulus novellus*, taken at 1 mm. intervals. ×5. A–D, AC 10305, LP_4, anterior end to right; E–H, AC 10311, RP_4. Note cement, interruption of enamel and presence of pulp cavity in last two sections. I–L, AC 10306, RP_4.

around the outside of the outer ring of enamel, increasing in thickness as the tooth is further worn until it almost surrounds the outer enamel as shown in Text-fig. 3H. As the base of the crown is reached, the enamel is interrupted at both anterior and posterior ends of the tooth, due to non-deposition of the enamel at this level.

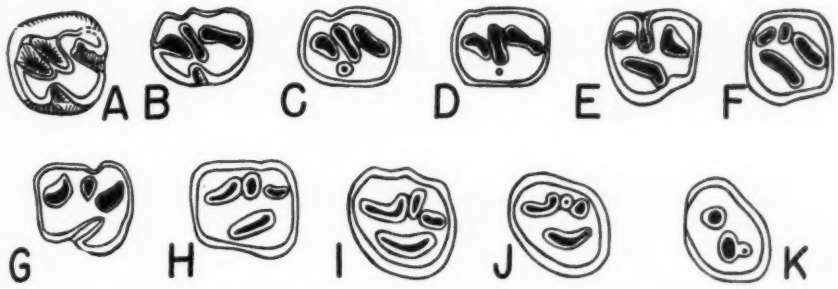
The variation seen in the lower premolars is not as great as that seen in the uppers and is primarily related to the relative shapes of the teeth. With the exception of the double mesofossettid in Text-fig. 3,J–K, the crown patterns are identical, each showing five lakes. The size range shown by the three individuals may appear extreme, but these are merely isolated specimens from a size continuum.

A number of specimens of M^2 show varying stages of wear. To complete the series of wear stages, one tooth (AC 10315) was sectioned to determine the variation which occurs late in an individual's life. Before sectioning, the mesostyle and metafossette were already lost, leaving four fossettes in two antero-posterior lines (Text-fig. 4A). The greatest variation occurred in the crown shape, which was initially nearly square, then rounded, then egg shaped, and finally almost triangular (Text-fig. 4,A–D). The four lakes persisted through the first two sections taken but, at the final section, three lakes were lost and only the hypofossette remained. At the last stage the enamel border was lost except on the lingual margin.

Three second lower molars (AC 11281, 11282 and 10323) were sectioned, because the first two shattered before all sections were completed. More variation in the lake pattern occurs in M_2 than in M^2. The order of lake formation depends upon the depth of the striids, which is variable. Hence in some teeth (Text-fig. 5,B and G) the protofossettid is the last lake formed while in another (Text-fig. 5E), the mesofossettid forms last. Lake size and reduction also is variable. In one tooth (Text-fig. 5,A–D), the protofossettid is never large and is the first lake lost, whereas in others (Text-fig. 5,E–F,G–K), the protofossettid is long and persists throughout the sections and the mesofossettid is a small circular lake which



TEXT-FIG. 4—Serial sections of second upper molar, *Mesogaulus novellus*, taken at 1 mm. intervals. AC 10315. ×5.



TEXT-FIG. 5—Serial sections of second lower molar, *Mesogaulus novellus*, taken at 1 mm. intervals. X5. A–D, AC 11282, RM_2, anterior and to right; E–F, AC 11281, RM_2, anterior end to right; G–K, AC 10313, LM_2.

is the first to be lost (Text-fig. 5,J–K). In this latter specimen, the protofossettid forms two lakes near the base of the crown (Test-fig. 5K). The shape of the parafossettid may vary with wear (Text-fig. 5,G–K) from an oval lake to an elongate L-shaped lake. The crown shape also changes with wear (see especially Text-fig. 5,G–K), from rectangular to oval.

The amount of variation in the details of the lake patterns in these specimens suggests that this may be normal in mylagaulids. If this is true, it is possible that some forms described as distinct species represent merely individual variants, although it is impossible to be certain without more data than are now available.

TOOTH HOMOLOGY AND REPLACEMENT

In the Split Rock collections, numerous mylagaulid teeth represent the entire cheek-teeth dentition with the exception of dP^3, but all are isolated teeth, which pose certain problems of identification. The discussion below is based on a study of the teeth in question and their comparison with skulls and jaws in the American Museum, as well as with published illustrations.

All authors agree that the mylagaulids have an unusual type of tooth replacement, but there has been considerable difference of opinion as to the homologies of the teeth that are involved. There is a large anterior tooth in both the upper and lower jaws, which is unquestionably the fourth premolar, although Dorr (1952, p. 322) considers that the lower tooth might be P_3, which does not seem reasonable since P_3 is otherwise unknown in the rodents.

Behind the permanent premolars, there are three teeth, in both the upper and lower jaws. The anterior of these is low crowned, and is shed fairly early in the life of the animal, either being pushed out by the premolar which gradually erupts, increasing in antero-posterior diameter as it does, or falling out to make room for the premolar. These teeth that are shed have been interpreted by Douglass (1903, p. 186) and by Dorr (1952, p. 323) as deciduous teeth (dP^4_4) and by Matthew (1924, p. 77) and McKenna (1955, p. 109) as M_1^1.

The two remaining teeth, in both upper and lower jaws, are very hypsodont. In some individuals only one of these may remain, but usually both are present. In most described mylagaulids, the two are subequal in cross section. In the Split Rock specimens, however, the posterior tooth is much the smaller.

In addition to these teeth, there are two anterior teeth in the upper jaw that are replaced by P^4 (Matthew, 1924, fig. 5, shows these teeth, but not clearly, in A.M.N.H. 18903, *Mylagaulus vetus*). The anterior of these is minute, and seems unquestionably to be dP^3. The other tooth has all the appearance of a rodent dP^4, including the spreading roots, and should be interpreted as that tooth. A single tooth in the lower jaw has the appearance of a rodent dP_4, again including the spreading roots, and was so identified by Matthew (1924, p. 81). Both Douglass (1903, p. 186) and Dorr (1952, p. 322) describe specimens in which only the posterior root of this tooth is preserved, which they call dP_3.

The only basis for interpreting this tooth as dP_3 is the interpretation of the tooth behind it, which is shed fairly early in life, as

dP_4. Douglass and Dorr accept this interpretation; Matthew, McKenna and the present authors do not. M_1, when unworn, has an elongate crown (Text-fig. 6A,8B, and Dorr, 1952, pl. 23, fig. 1), and a pattern identical with that of the tooth behind it. But the tooth is very low crowned, especially at the anterior end, and changes rapidly in shape with wear, so that it becomes compressed (Dorr, pl. 23, fig. 5), then highly compressed (cf. A.M.N.H. 18899 and Dorr, pl. 23, fig. 3) and then lost entirely (op. cit., pl. 23, fig. 6). This tooth is clearly being crowded against the enlarged premolar, and is gradually pushed out of the jaw as the premolar erupts. Dorr argues in considerable detail that the shedding of an anterior permanent molar is unusual and that therefore this tooth must be dP_4, making the one in front of it dP_3. Such a shedding would unquestionably be most unusual. On the other hand, the mylagaulids were unusual rodents and no other rodents are known that had two deciduous lower premolars. Dorr points out (op. cit., p. 322) the difficulties of understanding the ontogeny of an animal with a brachydont permanent tooth in the middle of a hypsodont field. This, however, is not completely convincing, because of our lack of understanding of the details of how tooth growth is controlled in any organisms. Moreover, if the deciduous premolars belong, phylogenetically, to the same tooth series as do the permanent molars, as is quite possible, there would very often be a change in hypsodonty in the middle of a homologous sequence. We, therefore, agree with Matthew that M_1^1 are temporary teeth in the Mylagaulidae, being pushed out by the large P_4^4 growing up beneath them. We agree with Dorr that Matthew (1924, p. 77) is probably in error in stating that the molars are deciduous progressively backward. Most mylagaulid jaws with mature dentitions show two teeth (or their alveoli) behind the premolars. There is, however, a possibility that one more is lost late in life, long after the loss of the first molars, some specimens apparently having only a single tooth behind the premolars. As indicated below, the material of *Mesogaulus novellus* shows M_3^3 to be greatly reduced in size, which may be the first stage in their phylogenetic loss. But it is illogical to argue, as does Dorr (1952, p. 325), that these teeth must be absent in the mylagaulids because they are absent in the cricetids, especially since this last statement is very questionable. Tooth homology in the cricetids is a problem beyond the scope of this paper.

In summary, then, the immature mylagaulids apparently possessed dP^{3-4} and dP_4. After these erupted, M_1^1 came into use. All these teeth were medium to low crowned. The next teeth to erupt (Text-fig. 6A and Dorr, 1952, pl. 23, fig. 1–2) would be M_2^2, followed at about the same time by M_3^3 and the permanent premolars. As the premolars erupted, the first molar would be pushed out, and the adult dentition of mylagaulids would be P_4^4, M_{2-3}^{2-3}.

SYSTEMATIC DESCRIPTION

MESOGAULUS NOVELLUS (Matthew)

Text-fig. 2–8

Mylagaulus novellus, Matthew, 1924.

Holotype.—A.M.N.H. 18911, fragmentary lower jaw with dP_4, P_4, M_{1-2} and broken incisor.

Referred specimens.—P^4—AC 10307, 10310, 10313, 10314, 10457; M^1—AC 10458, 11420; M^2—AC 10315, 10319–10321, 10468, 10469, 11300, 11414, 11423; M^3—AC 10324, 10325, 10327, 10331, 10333, 10336–10338, 10470–10477, 11303–11305, 11416–11418, 11424; P_4—AC 10305, 10306, 10308, 10309, 10311, 10312, 10456, 11301, Roy. Ont. Mus. Zool. Pal. 1931; M_1—AC 10460–10463, 11421, 11422; M_2—AC 10316–10318, 10322, 10323, 10335, 10464–10467, 10484, 11281, 11282, 11302, 11309, 11412; M_3—AC 10326, 10328–10330, 10332, 10334 10339, 10478–10482, 11283, 11284, 11306–11308, 11413, 11415, 11419, 11425, 11426, Roy. Ont. Mus. Zool. Pal. 1932; I_1—AC 10485–10487, 11310; dP^4—AC 10459; dP_4—AC 10483, 10488, 11427.

Diagnosis.—Typical *Mesogaulus*, with large mesostyle and normally five lakes in both P^4 and P_4; smaller than *M. praecursor* with smaller and lower crowned premolars; protocone nearer anterior end than in *M. praecursor*; mesostyle not as prominent as in the latter but still columnar; Y-pattern present in some upper premolars but not in others; M^2 nearly square; P_4 long and oval with no parafossettid; M_1 not compressed antero-posteriorly.

TEXT-FIG. 6—*Mesogaulus novellus*, A.M.N.H. 18911, holotype, left, ×5. A, crown view of dP_4–M_2; B, oblique view of P_4.

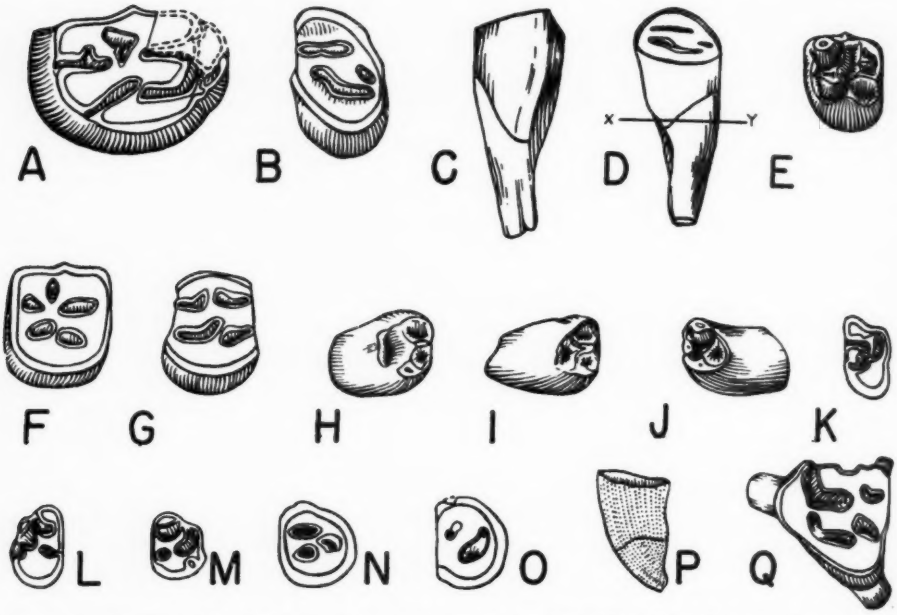
Horizon and localities.—Middle Miocene. Holotype from Sheep Creek beds, Sioux County, Nebraska. Referred specimens from vicinity of oreodont quarry (Schultz & Falkenbach, 1940, p. 251), seven miles by road northwest of Muddy Gap filling station, in a draw about ¼ mile south of U. S. Highway 280, Fremont County, Wyoming.

Discussion.—The holotype (Text-fig. 6) is clearly referable to *Mesogaulus*. The patterns of the four teeth are indistinguishable from those of the isolated specimens from Wyoming, and the measurements of the holotype all fall within the range of variability of the Wyoming population. The latter, therefore, clearly should be referred to *M. novellus*. The Wyoming specimens, found in a series of ant hills over a vertical range of one hundred feet, are all conspecific. The specimens range from well worn teeth to completely unworn ones. The premolars all are much lower crowned than in the other members of the genus but are sufficiently hypsodont to be easily distinguished from those of the more primitive genera, *Promylagaulus* and *Mylagaulodon*.

In crown pattern, the upper premolars are close to those of *Mesogaulus praecursor* Cook & Gregory (Text-fig. 2,7A). There are five lakes in the worn tooth with the parafossette generally showing the characteristic Y-pattern expected in a worn stage. The mesostyle is not as prominent as that of *M. praecursor* (Cook & Gregory, 1941, fig. 1), being only a slight projection near the middle of the buccal margin, and the parastria is poorly developed. The anterocone is merely part of an anterior crest, continuous with the protocone, as in some of the later members of the family, and in contrast to the condition in *M. praecursor*.

The two first upper molars are at quite different stages of wear. AC 11420, Text-fig. 7,B–D, is much higher crowned than AC 10458. In the former, there is a surface of interdental wear at each end of the tooth, with that at the anterior end much wider and deeper than that at the posterior, extending through the enamel to the dentine (Text-fig. 7B). This would result if M^1 and dP^4 erupted at approximately the same time and M^2 erupted much later, shortly before M^1 and dP^4 were lost. M^1 would then be in contact with M^2 for a shorter time than with dP^4, thus explaining the much greater wear at the anterior end. Both of the first upper molars have their roots compressed antero-posteriorly and concentrated under the posterior half of the tooth (Text-fig. 7,C–D), with a concave surface toward P^4. One striking difference between these two teeth is that, whereas there are four fossettes in the more worn tooth (AC 10458), there are only three in the less worn one (AC 11420). Additional wear in the latter could result in a division of the lingual lake to form four, and, with a slight shift of the parafossette toward the interior, the condition found in AC 10458 would be reached. With still more wear, either tooth would reach the stage shown by Douglass (1903, fig. 26c and 28), which is extremely compressed antero-posteriorly. Such a stage would be reached if the tooth were worn down to the line x–y in Text-fig. 7D.

Selected wear stages of the second upper molars are illustrated in Text-fig. 7,E–G. The teeth are hypsodont, with the mesostyle persisting for about one quarter of the tooth height. The posterior side of the tooth tends to be concave vertically due to the posterior displacement of the growing tip of the teeth. This may be due to pressure from the premolar. The teeth also curve somewhat lingually due to the presence of the orbit above and external to them. The crown is nearly square throughout but, in older animals, the anterior and posterior



TEXT-FIG. 7—Upper teeth of *Mesogaulus novellus*, ×5. A, AC 10313, P^4 right, anterior end to right; B–D, AC 11420, M^1 left. B, crown; C, lateral view with anterior end to right; D, median view. E, AC 11300, M^2 left; F, AC 10319, M^2 right, anterior end to right; G, AC 10321, M^2 right, anterior end to right, showing shortening of tooth through interdental wear; H, AC 11424, M^3 right, anterior end to right; I, AC 10476, M^3 right, anterior end to right; J, AC 10336, M^3 left; K, AC 11306, M^3 left; L, AC 10474, M^3 right, anterior end to right; M, AC 11303, M^3 left; N, AC 10327, M^3 left; O–P, AC 10472, M^3 left. O, crown view; P, median view, showing base of enamel, covered by cement. Q, AC 10459, dP^4 left.

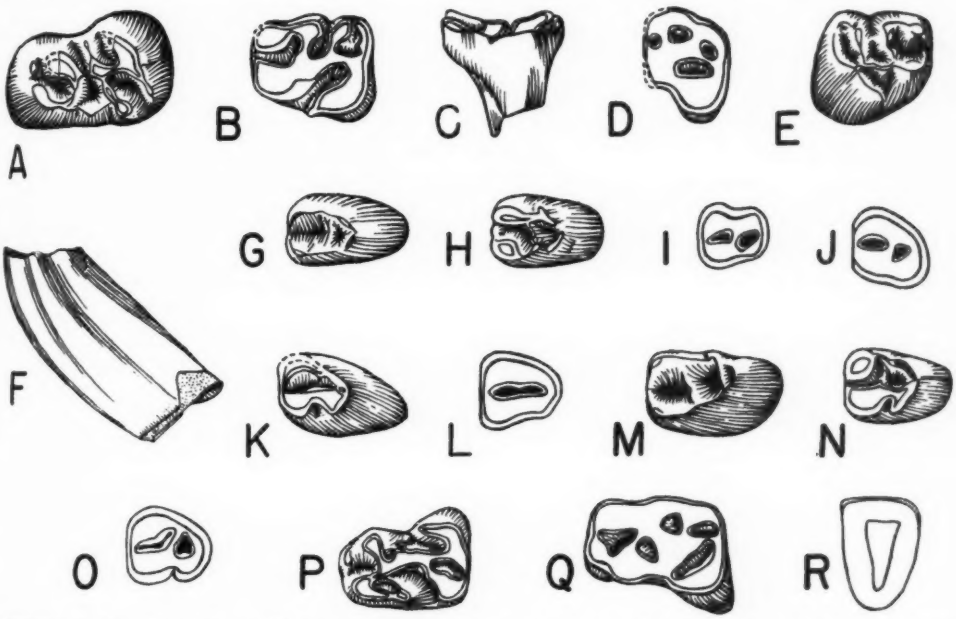
ends were worn away against P^4 and M^3, respectively. This shortening of the crown does not show up in the serial sections (Text fig. 4), since these teeth were not in use long enough to permit interdental wear. In unworn teeth (Text-fig. 7E), the fossettes are already isolated from the margins of the tooth. There are five of these, although the protofossette and parafossette are united. With slight wear (Text-fig. 7F), five fossettes are present, but the mesofossette is lost with very little additional wear (Text-fig. 4A) and the four fossettes persist nearly to the base of the tooth (Text-fig. 4C).

The third upper molars (Text-fig. 7,H–P) are elongated prisms, much smaller in diameter than the other upper teeth. There is considerable variation in the crown pattern, although basically there seems to be, anteriorly, a large protocone, a fairly large paracone, and a fair-sized protoconule, separated by two lakes, the parafossette and protofossette. The posterior end of the tooth is more variable, but there is normally a posterior ridge, more or less continuous with the paracone and protocone, surrounding a metafossette (Text-fig. 7,H–J). With wear, the cusps are cut down, and the three lakes persist (Text-fig. 7,K-N), although subsequent wear may eliminate the protofossette (Text-fig. 7,O). This last tooth is worn down almost to the cement cap that covers the lower end of the enamel (Text-fig. 7P). Interdental wear has completely cut away the enamel from the front of this tooth.

The lower premolars show the characteristic long, oval shape of those of the other species of *Mesogaulus* (Text-fig. 3,6B,8A). There seem to be no striking specific differences between these teeth and those of other species, except for the small size and low crown of *M. novellus*. This perhaps is because this species is earlier than most other members of the genus. In the unworn tooth (Text-fig. 6B,8A), the metafossettid opens onto the posterior edge of the tooth, farther to the rear than in *Mylagaulus vetus* (Cook &

Gregory, 1941, fig. 1) and the anterofossettid extends more posteriorly than they have shown. Otherwise, the lower premolars seem to be identical to those of the other species. The unworn lower premolar consists of four diagonally arranged crests separated by three deep fossettids, nearly or quite isolated from the margins of the tooth (Text-fig. 8A). Buccally, the protoconid, hypoconid and mesoconid are projected to the margin of the tooth, and are separated by deep flexids, which, upon wear, become fossettids (Text-fig. 3,8A). The protoconid and metaconid are united at their posterior margins, and are connected anteriorly, but less firmly, through the anteroconid. This results in variation as to the time of isolation of the anteroflexid to form an anterofossettid. The ectolophid is a strong ridge connecting the protoconid, mesoconid and hypoconid. The mesoconid is extended lingually as a mesolophid, to unite with the entoconid. There is a connection between the mesolophid and the metaconid, which is sometimes along the lingual margin of the tooth (Text-fig. 3A,8A) and is sometimes a short distance buccad of this point, so that a valley remains, which may even be temporarily isolated as a lake (Text-fig. 3,I-K). The hypoconid is continued into the hypoconulid, of varying distinctness. With wear, there may be very considerable variation in the shape of this tooth, as shown by the serial sections (Text-fig. 3).

The first lower molars show the change of pattern with wear very clearly. In the least worn (Text-fig. 8B), none of the flexids have been isolated as fossettids. In the holotype (Text-fig. 6A), the anterofossettid is isolated and split into two lakes. The metafossettid is also isolated, and the meso- and protoflexids have almost become isolated. The enamel has been removed from the front of this tooth by interdental wear. Other specimens show further wear, the ultimate (Text-fig. 8D) having three small lingual lakes and a large buccal protofossettid. Interestingly enough, the enamel is still complete along the anterior face of this tooth. In general crown shape and length



TEXT-FIG. 8—Lower teeth of *Mesogaulus novellus*, ×5. A, AC 10308, unworn P_4 right; B–C, AC 10463, M_1 left. B, crown view; C, median view. D, AC 10461, M_1 right, reversed image; E, AC 10322, M_2 right, unworn, anterior end to right; F, AC 10318, M_2 right, lingual view; G, AC 10328, M_2 right; H, AC 11307, M_3 right; I, AC 10329, M_3 right, crown outline only; J, AC 11284, M_3 left, crown outline only; K, AC 10478, M_3 left; L, AC 10479, M_3 left, crown outline only; M, AC 10480, M_3 left; N, AC 11415, M_3 left; O, AC 10334, M_3 left, crown outline only; P, AC 10488, dP_4 right; Q, AC 10483, dP_4 left; R, AC 10487, I_1 left, seen from rear.

the first lower molars strongly resemble the first upper molars but are less high crowned. The antero-posteriorly compressed root lies beneath the posterior half of the tooth and is concave anteriorly (Text-fig. 8C). The unworn teeth show a greater antero-posterior than transverse diameter, but the proportions change with wear (cf. Text-fig. 8,B-D). In some of the specimens the mesostriid extends well down the tooth, whereas the other fossettids are cut off very early. In one tooth the protostriid extends farther than the mesostriid. This seems to be another type of individual variation which results in different times of fossettid formation. The large preponderance of unworn or slightly worn specimens of this tooth probably indicates that it was shed very early in the life of the animal, after relatively little wear.

The second lower molars range from unworn teeth (Text-fig. 8E) through slightly worn teeth as in the holotype (Text-fig. 6A) and AC 10318 (Text-fig. 8F) to very worn teeth, with patterns like those shown by the serial sections (Text-fig. 5). The unworn crown pattern is identical with that of M_1, but the teeth are much more hypsodont. As in the case of M^2, the teeth are of nearly uniform cross section throughout and the root end is often (though not always) rotated posteriorly (Text-fig. 8F). This may indicate variable compression on the developing tooth germs from the growing P_4. There is considerable variation in the size and arrangment of the individual lakes, both throughout the life of an individual and between individuals (Text-fig. 5). The striids on the lingual side of the tooth vary both in persistence and in number. In one extreme (Text-fig. 8F) the mesostriid persists almost to the base of the tooth and an anterior striid persists three fourths of the length. In other specimens the anterior striid is not present at all and the mesostriid is relatively short.

The specimens of M_3 show a wide range of wear and exhibit extreme individual variation. A typical tooth (Text-fig. 8G) shows two enamel basins (probably the anterofossettid and the mesofossettid) surrounded by cusplets. Progressive wear (Text-fig. 8,H-J) gives a prism containing two small fossettids, which persist throughout life. Several variants from this type occur. In one, the crest between the two fossettids (metalophid) is incomplete (Text-fig. 8K) so that with wear there is a single elongate fossettid, lasting nearly or entirely throughout the life of the tooth (Text-fig. 8L). Another variant is the presence of a small third fossettid (metafossettid?) which is clearly ephermeral (Text-fig. 8M) and, in some other specimens, is indicated only by a slight irregularity of the posterior slope of the tooth (Text-fig. 8H). In some specimens, there is a protostriid between the protoconid and hypoconid (Text-fig. 8,K, N,O), which persists for a considerable period of time. Generally the anterofossettid is straight, but sometimes it curves around the rear side of the metaconid (Text-fig. 8,H,N,O). The posterior face of the tooth is rotated sharply backward. This can be recognized also in the holotype, where the alveolus of this tooth is nearly horizontal.

The extreme variability of M_3^3 suggests that these teeth were of little value to their owners, so that variants were of no selective disadvantage. This almost certainly indicates that the teeth are phylogenetically about to be lost, and is the main basis for assuming that M_3^3 are the second permanent teeth in the series to be lost, rather than M_2^2 as proposed by Matthew.

There is one fourth upper deciduous premolar in the collection (Text-fig. 7Q), similar in general appearance to that of *Mylagaulus vetus* figured by Matthew (1924, fig. 5). The tooth is worn considerably but the paraflexus has not yet been cut off to form a parafossette. The three roots diverge from the base of each corner of the approximately triangular tooth. This divergence, in contrast to the situation in M^1, is a strong indication that the tooth we identify as M^1 is not a deciduous tooth. The roots in dP^4 spread more than in dP_4 because the crown of the erupting P^4 is as wide as it will ever be, whereas the crown of P_4 when it erupts is only about one half as long as it will later become. There is a strong wear surface on the posterior face of dP^4, indicating a prolonged contact with M^1, and there is a much weaker wear surface just lingual to the anterior root, undoubtedly due to dP^3, although this tooth has not been recognized in the collection.

The deciduous fourth lower premolar is present in the holotype, and there are

three from Wyoming (Text-fig. 6A,8,P-Q). They are nearly rectangular with the anterior transverse width slightly less than the posterior. The hypoflexid is a long, diagonal valley near the posterior end of the crown, cut off as a hypofossettid in two of the specimens. Buccal to it lies the metaflexid, a large L-shaped basin in the holotype, and smaller in the other specimens. The mesofossettid of the holotype is large and complex, only just separated from the lingual margin of the crown. In AC 10488 (Text-fig. 8P), it is a long flexid, partly dammed near its middle. Its anterior end is isolated by a cross crest from the mesostylid, and further wear would produce the extra lake seen in this region in the holotype (Text-fig. 6A). The entire mesofossettid is a small triangular basin in AC 10483 (Text-fig. 8Q), with no trace of the extra lake. The protofossettid and anterofossettid are similar in all specimens, In the unworn tooth (Text-fig. 8P), the anteroflexid opened anteriorly, and the protoflexid was a branch of the hypoflexid.

The lower incisor has a broad, flat anterior face. That of the holotype is badly broken, and little or nothing can be told about it, except that the pulp cavity is large. Among the Split Rock specimens, there are six lower incisors that agree with that of the holotype. The anterior face is flat and the thin enamel extends only a very short distance onto both median and lateral sides of the tooth. The pulp cavity is extremely large, and somewhat pinched in near the middle (Text-fig. 8R). One very unusual feature is that the pulp cavity was open all the way to the wear surface. The incisor lies median to the root of the lower premolar, rather than going ventral to it as in most rodents.

The measurements indicate that *Mesogaulus novellus* is significantly smaller than *M. praecursor*, the smallest species previously referred to the genus. The significance of the size differences was computed using the method of Simpson and Roe (1939, p. 188–190) for comparison of a single specimen (in this case *M. praecursor*) with a larger sample, here the Wyoming specimens of *M. novellus*. The results shown in Table 1 clearly demonstrate that the specimens of *M. praecursor* belong to a different population from that including the specimens of *M. novellus*.

The measurements of Table 2 also demonstrate that there is no significant difference in size between the holotype of *M. novellus* and the Split Rock population, and that the latter represents a single, homogeneous population. In most measurements, the holotype falls within the observed range of the Split Rock specimens, and in all cases within two standard deviations of the mean of the Split Rock material. Two teeth, one M^3 and the other M_1, were not included in the measurements in Table 2. The former is a case of abnormal wear, which has cut the crown in such a way that all the measurements are much greater than in any other tooth. Careful inspection, however, shows that these apparent differences are not significant. The lower molar was omitted because it is highly worn, and, when this occurs, the tooth becomes very short anteroposteriorly. When these corrections are made, the V-values show a uniform population except in the case of the third molars. This is presumably because these teeth are nearly ready to be lost, phylogenetically. The V-values are small in P^4 and I_1, indicating that five specimens is not an adequate sample of a mylagaulid population. In analyzing measurements of mylagaulid molars, one must be careful to eliminate the effects of interdental wear in shortening the crowns of the teeth. Transverse measurements of the molars, at least, would therefore be more likely to be significant.

Relationships.—Mesogaulus novellus is

TABLE 1.—COMPARISON OF MEASUREMENTS OF *M. praecursor* WITH WYOMING *M. novellus*

	M. novellus		*M. praecursor*			
	Mean	σ		d	d/σ	P
Length P^4	5.07	.30	7.70	2.63	8.77	$<.001$
Width P^4	3.51	.12	4.20	.69	5.75	$<.001$
Length P_4	5.44	.33	7.90	2.46	7.45	$<.001$
Width P_4	2.85	.26	5.90	3.05	11.73	$<.001$

TABLE 2.—MEASUREMENTS OF *M. novellus*

		Holotype,	Split Rock specimens			
		A.M.N.H. 18911, left	N	M	σ	V
P_4	anteroposterior	4.90	8	5.44	.33	6.1
	transverse	2.65		2.85	.26	9.1
M_1	anteroposterior	2.64	5	2.73	.12	4.8
	transverse	2.35		2.29	.07	3.1
M_2	anteroposterior	2.40	16	2.88	.26	9.0
	transverse	2.24		2.26	.22	9.7
M_3	anteroposterior		20	1.95	.22	11.2
	transverse			1.73	.20	11.5
I_1	anteroposterior	2.75	5	2.88	.06	2.1
	transverse	ca. 1.85		1.96	.06	3.1
dP_4	anteroposterior	3.70	3	3.49		
	transverse	2.65		2.43		
P^4	anteroposterior		4	5.07	.30	5.9
	transverse			3.51	.12	3.4
M^1	anteroposterior		2	2.35		
	transverse			2.95		
M^2	anteroposterior		9	2.54	.22	8.7
	transverse			2.60	.20	7.7
M^3	anteroposterior		20	1.67	.21	12.6
	transverse			1.95	.21	10.7
dP^4	anteroposterior		1	3.30		
	transverse			2.80		

smaller and hence presumably more primitive than any other species of this genus. Unworn first upper and lower molars are longer than wide, which is also a primitive character. The forward position of the protocone and the small size of the mesostyle suggest more advanced characters. Perhaps *Mesogaulus novellus* is a sideline from the main evolutionary direction of the genus.

Age of locality.—Schultz & Falkenbach (1940, p. 250) state that this locality is Miocene but do not attempt to be more precise. The Wyoming material is presumably essentially the same age as the holotype (Sheep Creek) and all would probably be slightly, but only slightly, later than *Mesogaulus praecursor* from the Upper Harrison. The Split Rock locality is therefore probably lower Hemingfordian (Wood, H. E., et al., 1941, p. 12) in age.

REFERENCES

COOK, H. J., & GREGORY, J. T., 1941, *Mesogaulus praecursor*, a new rodent from the Miocene of Nebraska: Jour. Paleont., vol. 15, p. 549–552.

DORR, J. A., JR., 1952, Notes on the mylagaulid rodent dentition: Annals Carnegie Mus., vol. 32, p. 319–328.

DOUGLASS, E., 1903, New vertebrates from the Montana Territory: Annals Carnegie Mus., vol. 2, p. 145–199.

MATTHEW, W. D., 1924, Third contribution to the Snake Creek fauna: Am. Mus. Nat. Hist. Bull., vol. 50, p. 59–210.

MCGREW, P. O., 1941, The Aplodontoidea: Field Mus. Nat. Hist., Geol. Ser., vol. 9, p. 3–28.

MCKENNA, M. C., 1955, A new species of mylagaulid from the Chalk Cliffs local fauna, Montana: Wash. Acad. Sci., Jour., vol. 45, p. 107–110.

SCHULTZ, C. B., & FALKENBACH, C. H., 1940, Merycochoerinae, a new subfamily of oreodonts: Am. Mus. Nat. Hist., Bull., vol. 77, p. 213–306.

SIMPSON, G. G., & ROE, A., 1939, Quantitative zoology: McGraw Hill Book Co., New York, 483 p.

STIRTON, R. A., 1935, A review of the Tertiary beavers: Univ. Cal. Publ., Bull. Dept. Geol. Sci., vol. 23, p. 391–458.

WOOD, H. E., CHANEY, R. W., CLARK, JOHN, COLBERT, E. H., JEPSON, G. L., REESIDE, J. B., JR., & STOCK, C., 1941, Nomenclature and correlation of the North American continental Tertiary: Geol. Soc. Am., Bull., vol. 52, p. 1–48.

MANUSCRIPT RECEIVED DECEMBER 6, 1955.

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 685–694, 4 TEXT-FIG., MAY 1956

DENDRASTER: A PROBLEM IN ECHINOID TAXONOMY

D. M. RAUP
Division of Geological Sciences, Harvard University

ABSTRACT—Intraspecific variation in the echinoid genus *Dendraster* is studied by means of a statistical analysis of variation in the living species: *D. excentricus*. The character "eccentricity" is analyzed in samples from 34 collections of *D. excentricus*. This character is prominent in current classifications of the genus.

It is found that observed eccentricity data are biased by an allometric relation between eccentricity and test length. This allometry is described by an empirically derived curve. The parabolic function defining this allometric curve is used to eliminate the length bias from the eccentricity data.

No systematic geographic variation is recognized in *D. excentricus* as reflected in the character eccentricity. However, the species may be divided into two ecological races on the basis of eccentricity. The race inhabiting sheltered bays is significantly less eccentric than the race living along the open coast.

The eccentricity data for *D. excentricus* are employed in a review of the classification of the fossil members of the genus. The heretofore unrecognized allometry and ecological variation in *Dendraster* may explain some of the difficulties encountered in the fossil classification. It is found that there are greater differences in eccentricity between populations of *D. excentricus* than there are between species in the fossil record.

INTRODUCTION

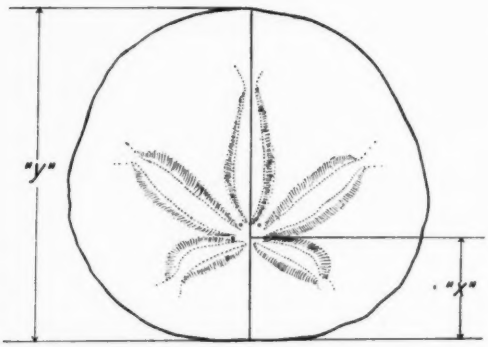
THE writer is currently engaged in a study of problems of intraspecific variation and species evolution in the echinoid genus *Dendraster* L. Agassiz. *Dendraster* is a sand dollar of the scutellid type and has a geologic range from the lower Pliocene to the Recent. Throughout this range, the members of the genus are restricted to the Pacific Coast of North America. About 25 species and subspecies are usually assigned to the genus and most of these have been catalogued by Grant & Hertlein (1938) in their work on the Cenozoic Echinoidea of Western North America. A few additional species have been described in the last few years by H. L. Clark (1948) and J. Wyatt Durham (1949, 1950). The living species have been discussed in some detail by Mortensen (1948, p. 380–385).

Dendraster excentricus (Eschscholtz), the only common living species of the genus, is found in the near-shore environment from southern Baja California to Vancouver Island in British Columbia. This species lives on sandy bottoms from the ebb-zone to a depth of about 90 meters and is abundant throughout its geographic range. *D. excentricus* has been chosen for intensive study of intraspecific variation because of its accessibility and because its ecology can be studied in a way not possible in fossil populations. It is hoped that the knowledge gained from this study may be applied to problems of classification, evolution, and paleoecology of the genus as a whole. This paper represents only a part of the study: that part dealing with variation in the eccentricity of the apical system.

The data presented here are based on the study of collections made by the writer during the summer of 1954 and of collections on loan from the University of California at Berkeley and from the Museum of Comparative Zoology at Harvard College. The writer wishes to express his sincerest thanks to the following persons who have critically read the manuscript and have offered many helpful suggestions: Dr. Bernhard Kummel, Dr. J. Wyatt Durham, Dr. John Imbrie, Dr. H. B. Whittington, and Dr. Ernst Mayr.

ECCENTRICITY

The posteriorly eccentric position of the apical system in the adult is one of the chief characters setting the genus *Dendraster* apart from other scutellid echinoids. Furthermore, many of the distinctions between species are based in large part on the eccentricity of the apical system. Eccentricity is usually expressed in terms of the position of the center of the apical system relative



TEXT-FIG. 1—Measurement of the eccentricity of the apical system. x equals the postero-apical distance and y equals the antero-posterior diameter.

to the mid-point of the antero-posterior diameter of the test (Kew, 1920, p. 114; Woodring, et al., 1940, p. 82). Since sand dollars of the *Dendraster* type are rarely circular in outline, any such measure of eccentricity is partially dependent upon the shape of the test. Despite variation in shape, however, a nearly perfect bilateral symmetry about the antero-posterior diameter is maintained and thus the choice of this dimension as a reference for eccentricity seems valid.

The measure of eccentricity adopted here is the ratio obtained by dividing the distance from the posterior margin of the test to the center of the apical system by the "radius" of the test (see Text-fig. 1). The center of the apical system is arbitrarily taken as the mid-point of an imaginary line connecting the two posterior genital pores and the "radius" of the test is one-half the antero-posterior diameter. The resulting ratio thus may vary from zero (apical system marginal) to one (apical system centered). In determining the eccentricity values to be analyzed in this paper, the two dimensions were measured to an accuracy of plus or minus 0.5 millimeter.

SAMPLING

The thirty-four collections of *Dendraster excentricus* utilized were made at scattered localities from Bahia San Quintin, Baja California to Orcas Island in Puget Sound. About a third of the collections were made by collecting specimens alive from shallow-water sites in sheltered bays. In samples from these collections there can be little doubt that all of the individuals were drawn from a single population. Most of the remaining collections, however, represent assemblages of bleached tests collected from beaches exposed to heavy surf action. Two questions immediately arise: are all of the specimens in a given beach collection drawn from one live population, and to what degree has selective transport introduced a bias into the beach samples?

Field evidence tends to support the view that a beach collection made within a limited area does represent a sample of a single population. For example, at each of two localities near Tillamook, Oregon, sand dollars were absent or present only as scattered fragments on the higher strand lines whereas small offshore bars, when exposed at low tide, were littered with undamaged tests—and in rare instances, live specimens; thus suggesting that sand dollar tests can withstand little transport in the surf zone. Furthermore, the tests were localized on these bars—a localization not easily explained by differential current action—suggesting that they had been derived from distinct populations offshore. The picture afforded by the two Tillamook localities is typical of beach sites all along the Pacific Coast and thus it seems fairly certain that the beach collections represent samples from single populations.

The statistical data to be discussed later also support this view in that the range of variation in eccentricity (as measured by the standard deviation of the mean) is essentially the same for all collections—whether beach or bay—while the means themselves vary significantly. It would be expected, were beach collections derived from more than one population, that their standard deviations would vary and would tend to be greater than those of the bay collections.

The mean size of an assemblage of sand dollars deposited on a beach will certainly be dependent in part upon sorting during transport, whereas other characters such as mean peristome width probably will not be biased by such sorting. Whether eccentricity itself is responsible for the sorting action during transport cannot be decided without comparing "live" collections from below the surf zone in a given area and collections

from the beach adjacent to it. However, there is no indication that any sorting during transport is effected by eccentricity or any characters thus far determined to be related to eccentricity—with the exception of size, which will be discussed below. Lacking positive evidence to the contrary, therefore, the assumption is made that eccentricity does not introduce a bias into the beach samples.

The sample size used in most instances in the analysis of eccentricity for the 34 collections of *D. excentricus* was 25. Although admittedly small, this sample size was chosen as a standard partly because collections from many localities were limited, and partly because repeated sampling from a few large collections showed negligible differences between samples of one collection. The statistical methods employed will be discussed as they are presented.

ANALYSIS OF DATA

The data from the 34 collections of *D. excentricus* were analyzed statistically to determine the nature and degree of intraspecific variation in the single character: eccentricity. Before this could be done, however, an apparent allometric relation between length and eccentricity had to be explored. It was recognized early in the study that there is a significant correlation between eccentricity and length (antero-posterior diameter) in many populations of the species. In some samples it was observed that eccentricity increases with increasing length and in others, it decreases with increasing length. Since the size distribution of the specimens varies greatly from sample to sample, this relation between eccentricity and length (or size) could not be ignored in comparisons of eccentricity values for different collections.

Therefore, 15 typical samples of *D. excentricus* were analyzed in an effort to derive an expression for this allometry which could be used as a correction for all the raw eccentricity data. The 15 samples were chosen from the 34 collections to include the geographic extremes, the extremes in mean length, and as wide a range of environment as possible. Each sample contained 25 specimens.

The data for each of these samples were then analyzed separately: with antero-posterior diameter (y) being plotted against postero-apical distance (x). Without exception, the correlation between these two dimensions for single samples was high. Typical correlation coefficients (r) are given in Table 1. On the strength of this, reduced major axes were calculated for each sample, using the following formula:

$$y' = \frac{\sigma_y}{\sigma_x} x' + \left[\bar{y} - \left(\frac{\sigma_y}{\sigma_x} \right) \bar{x} \right]^*$$

The relation between antero-posterior diameter (length) and postero-apical distance for each sample was thus expressed by a straight line equation in the form:

$$y = ax + b \qquad (1)$$

where: y is the antero-posterior diameter, x is the postero-apical distance, and a and b are constants.

The reduced major axis was used in preference to the conventional regression line because it is not possible to determine the dependent and independent variable when

TABLE 1.—CORRELATION COEFFICIENTS (r) FOR THE ASSOCIATION BETWEEN ANTERO-POSTERIOR DIAMETER (y) AND POSTERO-APICAL DISTANCE (x) IN 15 SAMPLES OF *D. excentricus*

Locality no.	Sample Size (n)	(r)*
1	25	0.88
2	25	0.86
4	25	0.95
5	25	0.92
7	25	0.92
9	25	0.87
11	25	0.96
12	25	0.98
16	25	0.90
17	25	0.94
21	25	0.92
26	25	0.82
27	25	0.86
30	25	0.74
31	25	0.84

$$*r = \frac{p}{\sigma_x \sigma_y}$$

where:

$$p = \frac{\Sigma(XY)}{N} - \left[\frac{\Sigma(X)}{N} \right] \left[\frac{\Sigma(Y)}{N} \right]$$

* Kermack & Haldane, 1950, p. 30.

UNIVERSITY OF MICHIGAN LIBRARIES

dealing with two dimensions such as x and y.

Eccentricity was defined earlier as the ratio between the postero-apical distance and half the antero-posterior diameter. Using the notation employed above, eccentricity (e) may thus be expressed as $x/\frac{1}{2}y$ or:

$$e=\frac{2x}{y} \tag{2}$$

therefore:

$$x=\frac{ey}{2} \tag{3}$$

Substituting this value of x (3) into equation 1, we have an expression for eccentricity in terms of length:

$$e=\frac{(2y-2b)}{ay} \tag{4}$$

By differentiating this equation we can derive an expression for the rate of change in eccentricity with respect to length:

$$\frac{de}{dy}=\frac{2b}{ay^2} \tag{5}$$

de/dy, therefore, may be used as a measure of the nature and extent of the allometric relation between eccentricity and length in a given sample. If de/dy is positive, eccentricity increases (numerically) with an increase in length and if negative, it decreases with an increase in length. It should be emphasized that the *smaller* the numerical value of eccentricity, the *more* eccentric the apical system.

de/dy was then calculated for each of the 15 samples (using mean values for y). There was quite a wide range of values for this "rate of change" in eccentricity: in two-thirds of the samples eccentricity decreased with length and in the remaining third it increased with length.

Although de/dy values express variation in the nature and degree of allometry from sample to sample, they do not provide a means of eliminating the length bias such that eccentricity values for various samples may be compared. It was found, however, that there was a significant correlation between de/dy and mean length in the fifteen samples ($r=0.61$). That is, the rate of change of eccentricity is a function of length. Assuming this to be a straight line function, a reduced major axis was calculated in terms of de/dy and y: the equation for this line takes the form:

$$\frac{de}{dy}=Ay+B \tag{6}$$

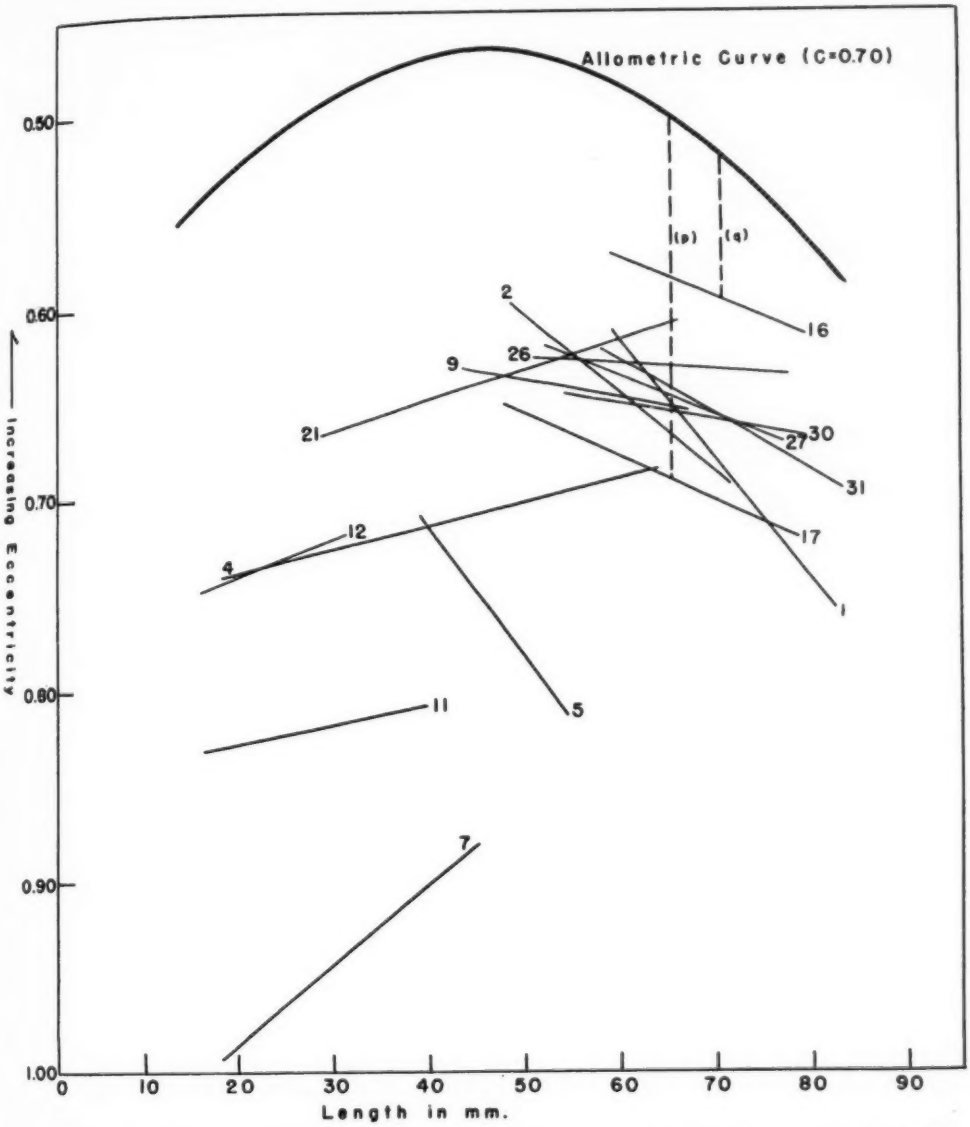
By integration of equation 6 we have:

$$e=\left(\frac{A}{2}\right)(y^2)+By+C \tag{7}$$

Let us consider this last equation, and the previous one, in light of our original objective: to derive a correction factor for the effect of size on eccentricity. Equation 2 only defines eccentricity in terms of the two dimensions: x and y. Equation 4 expresses eccentricity as a function of length (y) and two constants, a and b, which are different for each sample. This equation, therefore, can be of little help in equating raw eccentricity values. Similarly, equation 5 includes two constants which differ from sample to sample. By virtue of the correlation betwen de/dy and length, however, equation 7 provides us with an expression for eccentricity in terms of length and two constants (A and B) which are the same for all samples. The evaluation of C, the constant of integration, will be discussed below.

The curve in Text-fig. 2 represents eccentricity as a function of length, as plotted from equation 7, where C is arbitrarily assumed to be 0.70. This curve, then, expresses the allometric relation between length and eccentricity. It should be noted that in the smaller size ranges eccentricity is increasing, while in larger sand dollars this trend is reversed and eccentricity decreases. This curve was derived from analysis of only 15 samples but it is assumed that the same relationship holds for all of the 34 collections and perhaps for the species as a whole.

Also in Text-fig. 2, eccentricity is plotted against length separately for each of the 15 samples (using equation 4). Since de/dy is in part dependent on y, these 15 lines should be slightly curved, but, for the sake of simplicity, they have been plotted as straight lines (with the mean length value for each sample being used in the calculation of de/dy). In Text-fig. 2 it may be seen that the slopes of these fifteen lines fit quite well with the slope of the curve at their respective y values. This is not surprising since the slopes of these



TEXT-FIG. 2—General curve for the allometric relation between test length and eccentricity. Straight lines below the curve represent eccentricity plotted against length for fifteen samples of *D. excentricus*. See text for further explanation.

lines are nothing more than de/dy values and the curve was derived from de/dy and y for the same 15 sets of data. Absolute values of e, however, did not enter into the derivation of the curve (equations 6 and 7) and thus the obviously poor fit between the lines and the curve with respect to e is to be expected. Deviations from the curve as measured along the e-axis involve the evaluation of the integration constant, C. The effect of variation in C is to displace the curve vertically without changing its shape or its position relative to y. Thus, any two populations of *D. excentricus*, represented by any two of the straight lines in Text-fig. 2, may conform to the same pattern of

allometric growth but differ in absolute values of eccentricity. C, therefore, seems to control that part of observed eccentricity which is not due to the length allometry. Furthermore, C does not appear to be constant for all samples as shown by the differing e-deviations of the several lines from the curve in Text-fig. 2 (p and q, for example). Thus, we have a variable, C, which is a function of all the factors causing variation in eccentricity, whether they be genetic or ecological. A relative measure of this variation may be derived by arbitrarily assuming a value for C, as in Text-fig. 2, and noting the deviations in e of the several observed eccentricity values from the resulting curve. For example, it may be said that sand dollars from locality 16 (see Text-fig. 2) are more eccentric than those from locality 17 by a value (p-q) and that this difference is not due to a difference in size. In practice, the values for p and q may be calculated directly from equation 7 rather than determined graphically.

Using the method outlined above, the data from all of the 34 collections were "corrected" for the length allometry. The following equation, based on equation 7, was employed:

$$e_c = e_o - \frac{Ay^2}{2} - By - C \qquad (8)$$

where:

$A = 173 \times 10^{-6}$ (value from equation 6, above)
$B = 7882 \times 10^{-6}$ (value from equation 6, above)
$C = 0.15$ (arbitrary)
y = mean length
e_o = observed mean eccentricity
e_c = "corrected" mean eccentricity

Mean values were used for y, e_o, and e_c because the results were found not to vary significantly from results obtained where all the data were employed. The standard error of e_c is indeterminate and thus no attempt has been made in the presentation of the data to express the uncertainty of the "corrected" eccentricity values. The standard deviations of e_o (Table 2) and the correlation coefficient for de/dy and $\bar{y}$ (above) do, however, give some indication of the reliability of the e_c data.

In summary, the foregoing analysis has been designed to eliminate the effect of differential growth on observed eccentricity. This has been done by deriving a general curve from the observational data which expresses eccentricity as a function of length (equation 7). Knowing this function then, one can determine whether two given samples differ in eccentricity solely because of differing specimen length or whether they differ because of factors other than length. This may be determined either graphically, as in Text-fig. 2, or mathematically, using equation 8. The effect of this "correction" may be seen by an examination of Table 2, where, for example, the raw eccentricity value for locality 31 is higher than that for locality 30 whereas this relationship is reversed in the corrected eccentricities. Furthermore, the data for locality 30 are essentially unchanged by the correction whereas the e value for locality 31 is considerably altered.

The e_c values given in Table 2 are measured in the same units as those resulting from the original definition of eccentricity (see equation 2), but because C was fixed arbitrarily, the actual values of e_c have no meaning except when one value of e_c is being compared with another. Table 2 therefore provides a theoretically unbiased picture of the relative differences in eccentricity in 34 populations of *D. excentricus*. We are now equipped to discuss these differences in terms of intraspecific variation.

VARIATION IN ECCENTRICITY

From the data in Table 2 it may be seen that although the bulk of the corrected eccentricities is essentially the same, there are some instances where two values differ significantly. For example, the probable range in eccentricity for locality 16 is distinct from that for locality 17, as expressed by their mean corrected eccentricities and standard deviations (the latter being the standard deviations of e_o). The problem now is to determine what factor or factors control the variation. This can only be done by trial and error: examining likely factors in the ecology and distribution of *D. excentricus* in an effort to isolate those which control intraspecific variation.

Text-fig. 3 represents the corrected eccentricity data in terms of two readily defined characteristics of the species as a

TABLE 2.—ECCENTRICITY DATA FOR 34 SAMPLES OF *D. excentricus*

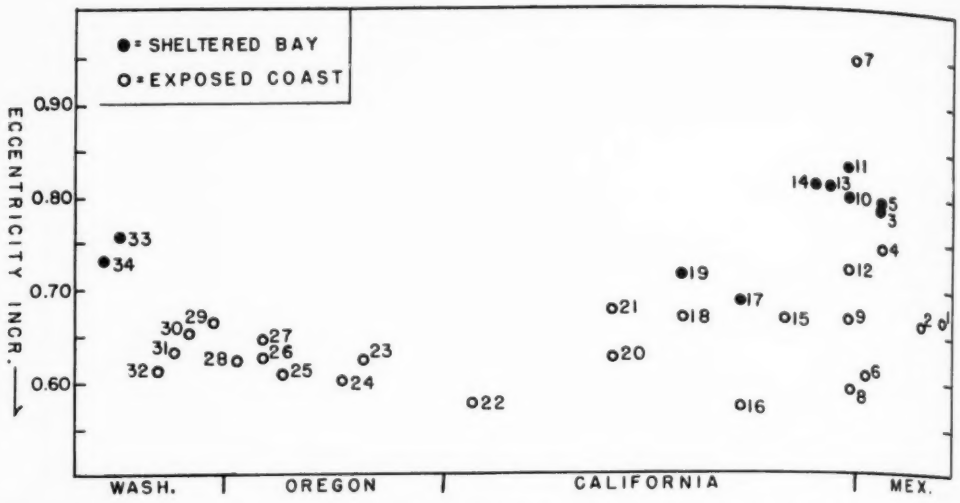
Locality	Loc. No.	Sample Size (n)	Mean Length ($\bar{y}$)	Mean Obs. Eccent. ($\bar{e}_0$)	Stan. Dev. of ($\bar{e}_0$)	Mean Corr. Eccent. ($\bar{e}_c$)
			Mexico			
San Quintin	1	25	71.2	0.696	0.046	0.668
Pta. S. Ysidro	2†	25	60.8	0.653	0.041	0.662
Ensenada	3	25	51.0	0.762	0.041	0.788
Ensenada	4	25	37.0	0.720	0.064	0.743
Ensenada	5	25	46.4	0.766	0.041	0.795
Rosarito Beach	6	25	66.3	0.616	0.035	0.608
Coronados Is.	7*	25	33.4	0.930	0.054	0.946
			California			
Coronado Beach	8*	5	78.8	0.658	0.030	0.591
San Diego	9	25	53.5	0.646	0.035	0.669
San Diego	10*	25	45.2	0.766	0.054	0.796
Mission Bay	11	25	26.3	0.823	0.046	0.830
La Jolla	12	25	21.2	0.742	0.035	0.720
Newport Bay	13*	25	41.9	0.782	0.054	0.810
Anaheim Bay	14*	8	50.6	0.784	0.021	0.811
Sta. Cruz Is.	15*	4	63.8	0.668	0.033	0.668
Morro Bay	16	25	70.6	0.597	0.020	0.572
Morro Bay	17	25	66.2	0.695	0.040	0.687
Monterey Bay	18†	25	55.6	0.650	0.035	0.670
Monterey Bay	19*	8	41.2	0.688	0.030	0.715
San Francisco	20*	12	67.2	0.640	0.034	0.628
Stinson Beach	21	25	38.0	0.655	0.046	0.679
Little River	22	25	72.4	0.612	0.029	0.578
			Oregon			
Charleston	23	25	64.9	0.629	0.046	0.625
Reedsport	24	25	67.2	0.613	0.041	0.602
Neskowin	25	25	65.7	0.616	0.035	0.610
Tillamook	26	25	65.3	0.634	0.041	0.629
Tillamook	27	25	64.2	0.648	0.029	0.647
Seaside	28	25	68.4	0.641	0.035	0.625
			Washington			
Cohasset	29	25	63.1	0.663	0.035	0.665
Ocean City	30	25	65.7	0.659	0.041	0.653
Moclips	31	25	72.2	0.666	0.020	0.633
Kalaloch	32	17	73.6	0.653	0.035	0.614
Orcas Is.	33†	25	67.6	0.769	0.035	0.756
False Bay	34†	25	76.2	0.785	0.046	0.732

* Collections from the Museum of Comparative Zoology at Harvard College.
† Collections from the University of California at Berkeley.

whole. In the figure, eccentricity is plotted against degrees of latitude. Since *D. excentricus* has essentially a linear distribution on the Pacific Coast of North America, latitude may be used as a parameter of the geographic distribution of the species. In addition, the points have been separated into two groups corresponding to the two most pronounced environments inhabited by sand dollars: the sheltered bay and the exposed coast. Text-fig. 3 shows that there is a well-defined distinction between bay and open coast forms as measured by eccentricity. This is particularly pronounced in the case of localities 16 and 17 where the two collection sites were within a half mile of each other; one (17) inside Morro Bay and the other (16) immediately outside the bay. A similar situation holds for localities 3, 4, and 5. Localities 3 and 5 lie on the sheltered side of a sand spit restricting a bay and locality 4 lies on the exposed side of the same sand spit, less than a quarter of a mile away. Although there seems to be a real distinction between bay-inhabiting sand dollars and those living below the surf zone on the exposed coasts, Text-fig. 3 shows no geographic trend within either of these groups.

It should be noted that locality 7 falls far from any of the above-mentioned points in Text-fig. 3. This is not surprising since

UNIVERSITY OF MICHIGAN LIBRARIES



TEXT-FIG. 3—Eccentricity as a function of latitude and environment in 34 samples of *D. excentricus*. Numbers refer to collecting localities (see Table 2).

locality 7 represents the only available collection of *D. excentricus* var. *elongatus* Clark. It is significant however, that Text-fig. 2 shows that the rate of change of eccentricity with respect to length conforms to the general allometric curve for the species. Thus, variety *elongatus* may be differentiated from typical *D. excentricus* on the basis of eccentricity but the patterns of relative growth of the two are indistinguishable.

SUMMARY AND INTERPRETATION OF ECCENTRICITY DATA

The statistical data presented above indicate that there is no geographically controlled variation in eccentricity in the 34 samples of *D. excentricus* which were analyzed. Since the 34 samples include collections from practically the whole range of the species, it is safe to conclude that there is no geographic variation in eccentricity for the species as a whole. This does not preclude the possibility, of course, that other characters are subject to geographic variation. Furthermore, this conclusion does not necessarily demonstrate that the species is a single interbreeding population.

The statistical data do indicate, however, that differences in eccentricity may be related to environment: the bay forms being consistently less eccentric than the open coast forms. It appears that we are dealing with two localized ecological races. The question is whether or not these two races are genetically different. A satisfactory answer to this question would require carefully controlled breeding and transplanting experiments which are beyond the scope of this study. In lieu of this, certain indirect evidence may be considered. Wherever colonies of the bay inhabiting race occur they are more or less contiguous with open coast populations. Furthermore, there does not seem to be any effective barrier between the environments which would prevent mixing of the races through larval dispersion or adult migration. Therefore, any basic genetic difference between the two races could not be maintained unless, of course, the races are actually distinct species. It does not seem reasonable to suppose that these are different species, and it is unlikely that any taxonomist would describe them as such on the basis of the subtle morphological differences. More likely the races are the result of phenotypic reaction to the environment on the part of the individual and do not represent any genetic change in the population.

If this is true, the difference between the races may be tentatively explained in terms of the normal feeding position of sand dollars. The feeding habits of *Dendraster* are

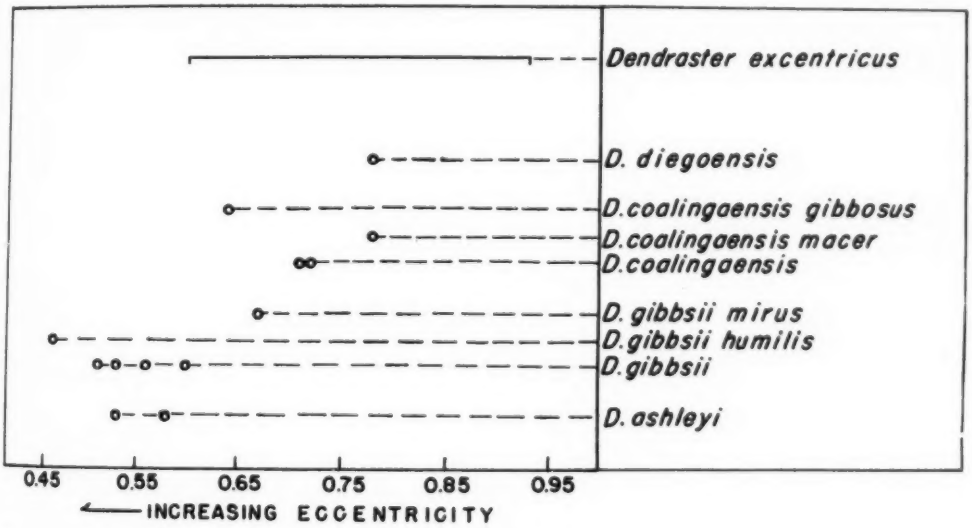
virtually unknown except that they feed on detrital organic material transported to them by currents. When the animal is not feeding, the test is flat, with the oral surface down, and may or may not be buried in the sand. In order to expose the peristome, periproct, and food grooves to nutrient-bearing currents, the test is inclined to the substratum with the posterior two-thirds exposed and the anterior third buried. The shift from the flat position to the inclined (feeding) position in response to tidal currents has been observed by the writer in several bays in Southern California and Mexico.

An increase in eccentricity would mean that the madreporite would be farther off the bottom when the sand dollar was in this position, or looking at it from another point of view, increased eccentricity of the apical system would allow the sand dollar to burrow deeper without obscuring the madreporite. In either case, increased eccentricity would benefit those sand dollars which inhabit areas where the bottom sediment is continually being stirred due to turbulence. Such areas would be more likely just below the surf zone on exposed coasts than in sheltered bays. The eccentricity data conform to this picture. In line with this interpretation, it would be interesting to see if eccentricity of the peristome parallels that of the apical system.

IMPLICATIONS REGARDING THE GENUS

The biometrical analysis presented in this paper provides a means of evaluating the classification of the fossil members of the genus *Dendraster* insofar as based on eccentricity. As mentioned earlier, eccentricity has figured prominently in the species classification of the genus. Furthermore, several other characters which have been used extensively may be shown to be correlated with eccentricity. Some of the characters dependent on eccentricity (or the reverse) are: the length of the test, the angle of the bivium, the shape and width of the paired posterior petals, and the length of the unpaired anterior petal. In making the distinctions between species, the allometric relations of sand dollars and their ecological variation have not been considered. Furthermore, fossil species have in several instances, of necessity, been described after the examination of only a few specimens from perhaps one or two localities. With these considerations in mind let us re-examine the *D. excentricus* data.

As may be seen in Table 2, the uncorrected mean values of eccentricity in *D. excentricus* range from 0.60 to 0.93: a range



TEXT-FIG. 4—Observed range in mean eccentricity for the modern species, *D. excentricus*, compared with mean eccentricity values for typical assemblages of several fossil species.

which includes typical eccentricity values for several of the fossil species (see Text-fig. 4). Also in Text-fig. 4, the fossil species *D. ashleyi* (Arnold), *D. gibbsii* (Remond), and *D. gibbsii humilis* Kew are all more eccentric than *D. excentricus* but the range in eccentricity for the three combined is less than that for the modern species. *D. ashleyi*, *D. gibbsii*, and *D. gibbsii humilis* are usually distinguished on the basis of two characters: eccentricity (or characters dependent upon it) and the relative thickness of the test (Kew, 1920, p. 116, 124). To cite another case, *D. gibbsii* is distinguished from *D. hesperis* Kew only by the eccentricity or such characters as the bivial angle (according to the description of Kew, 1920, p. 126), which vary directly with eccentricity. All of the species referred to above may be perfectly valid but in light of the data presented here this is doubtful.

Let us consider the classification of *Dendraster* in another light. The environmental differences between assemblages of fossil sand dollars are, of course, difficult if not impossible to recognize from the enclosing sediment and associated fauna alone. Thus, if the 34 assemblages of *D. excentricus* dealt with here were found as fossils in Tertiary rocks, the paleontologist could make a strong case for dividing them into two groups (possibly species) on the basis of eccentricity because the two ecological races are biometrically distinct enough to satisfy any requirements of statistical significance. It is quite possible therefore, that ecologically determined variants within a single species have been interpreted as separate species.

The lack of recognition of allometry in *Dendraster* may also be responsible for some of the difficulties encountered in the current classification of the genus. For example, two assemblages might be distinguished on the basis of eccentricity when actually there is only an apparent difference resulting from selection of the tests by size during transport. If, as is quite possible in dealing with fossil assemblages, the allometric relations between length and eccentricity were partially but not completely understood, a seemingly valid distinction could be made between sand dollars whose eccentricity increases with length and those whose eccentricity decreases with length (see Text-fig. 2). This distinction might even be considered to merit division at the generic level.

The biometrical analysis of *D. excentricus* thus has not only expanded the knowledge of a single species but it has also provided one means of studying the classification and phylogeny of the genus as a whole. Furthermore, this study has brought to light some of the difficulties encountered in distinguishing fossil species, either by qualitative or quantitative means.

REFERENCES

CLARK, H. L., 1948, A Report on the Echini of the Warmer Eastern Pacific, based on the coll. of the "Velero III": Alan Hancock Pacific Expeditions, vol. 8.

DURHAM, J. W., 1949, *Dendraster elsmerensis*, Durham, n.sp.: Am. Jour. Sci., vol. 247, p. 49–62.

——, 1950, 1940 E. W. Scripps cruise to the the Gulf of California, Pt. II, Megascopic Paleontology and Marine Stratigraphy: Geol. Soc. Am. Mem. 43, p. 1–216.

GRANT, U. S., IV & HERTLEIN, L. G., 1938, The West American Cenozoic Echinoidea: Univ. California Los Angeles Publ., Math. Phys. Sci., vol. 2, p. 1–225.

KERMACK, K. A., & HALDANE, J. S. B., 1950, Organic correlation and allometry: Biometrika, vol. 37, p. 30–41.

KEW, W. S. W., 1920, Cretaceous and Cenozoic Echinoidea of the Pacific Coast of North America: Univ. Calif. Berkeley Publ. Geol., vol. 12, p. 23–236.

MORTENSEN, TH., 1948, A Monograph of the Echinoidea: vol. 4, pt. 2, p. 1–471; C. A. Reitzel, Copenhagen.

WOODRING, W. P., STEWART, RALPH, & RICHARDS, R. W., 1940, Geology of the Kettleman Hills oil field, California: U. S. Geol. Survey, Prof. Paper 195, p. 1–170.

MANUSCRIPT RECEIVED DECEMBER 5, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 695–699, MAY 1956

THE CONODONT GENUS *PRIONIODUS* AND RELATED FORMS

F. H. T. RHODES AND KLAUS J. MÜLLER
University of Illinois, Urbana, and State University of Iowa, Iowa City

ABSTRACT—A new genus *Neoprioniodus* (type species: *Prioniodus conjunctus* Gunnell) is proposed to include those species formerly described as *Prioniodus* but which are now excluded from it by redefinition.

INTRODUCTION

IN A recent article Lindström (1954, p. 589) has redefined the genus *Prioniodus* Pander, because the original description was based upon fragmentary material. The consequent problems of nomenclature and taxonomy involved in this redefinition are somewhat complex and appear to stand in need of clarification.

The necessity of establishing a new genus was recognized independently by the present writers. When we recently met for the first time, we each discovered that the other had completed a manuscript, describing such a new genus. Both had arrived at precisely the same conclusions about morphologic details and had even selected the same name for the new genus. These independent conclusions gave us considerable satisfaction, for they seemed to emphasize that the need for the recognition of a new genus is a logical and necessary development of Öpik's (1936) and Lindström's (1954) investigations.

THE PREVIOUSLY ACCEPTED INTERPRETATION OF THE GENUS *PRIONIODUS*

Pander (1856, p. 29) originally defined the genus as follows (translated from German):

> Under this name we unite all those teeth or jaws in which a very big tooth arises, and to which on one or both sides a row of smaller ones is added. The hollow base extends lengthwise beneath all of these teeth up to a certain [neither very high, nor very low] height.

It will be noted that Pander's description of the genus was very broad. The three diagnostic characters were the large fang, the presence of a posterior bar sometimes accompanied by an anterior denticulated portion, and basal cavity that extended along the entire length of the unit.

The type species of the genus was designated by Miller (1889, p. 520) as *P. elegans* (Pander's first species). Branson & Mehl, however, suggested that this species should be regarded as atypical of the genus (1944, p. 241). However, in accordance with the Rules of Zoological Nomenclature, it is essential to maintain *P. elegans* as type. Pander described four other species of *Prioniodus*, in addition to *P. elegans*. These species represent a wide variety of forms. The specimens referred to these species by Pander seem to us to belong to the following genera:

1. *Prioniodus* s.s.: *Prioniodus elegans*, p. 29, pl. 2, fig. 22a,b;23 (22b is here designated holotype) and *Prioniodus elegans ?*, pl. A, opposite p. 20. fig. B,C. The latter forms show the characteristic three processes and are probably not conspecific.
2. *Neoprioniodus*, n. gen.: *Prioniodus tulensis* [part], p. 30, pl. 2A, fig. 1 (designated holotype by us, herein). This species is poorly known and the type specimens are lost. We have therefore not considered it to be a suitable type-species for *Neoprioniodus*.
3. *Ligonodina* Ulrich & Bassler: *Prioniodus tulensis* [part], p. 30, pl. 2A, fig. 18,19,?20. These figures are based on fragmentary material which is therefore not named specifically.
4. Genus indet. *a*: *Prioniodus carinatus*, p. 30, pl. 2, fig. 25 and *Prioniodus sulcatus*, p. 29, pl. 2, fig. 24a,b.
5. Genus indet. *b*: *Prioniodus volborthii*, p. 30, pl. A, opposite p. 20, fig. A. On the basis of the illustration and de-

scription it seems to be impossible to derive a modern generic determination. The specimen may represent *Prioniodina* or *Hibbardella*.

It is clear from the figured specimen which Hinde (1879, p. 356, ff.) has referred to *Prioniodus* that he regarded the genus as including forms with a posterior bar, large fang, and anticusp as well as those with two lateral bars and a lateral process extending from the fang.

As has been noted by Rhodes (1955) a number of later workers have given their own interpretations of the genus, and this has had the dual effect of both limiting the genus and also admitting those forms which would not have been included in Pander's original description. The two interpretations which have set the morphological standard for virtually all subsequent work are those of Ulrich & Bassler (1926) and Branson & Mehl (1933). The main features of these two descriptions of the genus are included in Table 1.

Branson & Mehl (1933, p. 129) studied specimens which they believed to be from the type locality of *P. elegans* and remarked that the anterior edge of the anticusp was

TABLE 1.—INTERPRETATIONS OF THE GENUS *Prioniodus* AS GIVEN BY A NUMBER OF AUTHORS

Author(s) and date of publication	Overall shape	Anterior fang			Anticusp	
		Size and shape	Edges	Anterior edge	Length	Anterior edge
Pander, 1856, p. 29		Very big				May be denticulated
Ulrich & Bassler, 1926, p. 8, 9	Pick-shape well developed	Relatively large	Both sharp	Nearly straight	(basal extension) Usually strong and often as long as cusp (fang) itself, although variable in length.	Nearly straight
Branson & Mehl, 1933, p. 129, 130	Pick-like appearance	Large Composed of several fused denticles			An extension of the anterior fang.	Presumably denticulate (1933, p. 130, line 1)
Fay, 1952, p. 16	Unit with one main cusp followed by smaller denticles, none of which are on the posterior edge of the main cusp.	Directed backward rather than forward.			Is almost in same plane as bar.	Smooth or denticulate

Author(s) and date of publication	Posterior Bar		Lateral Process	basal cavity	Remarks
	General form	Denticles	Present and general form		
Pander, 1856, p. 29		A row of smaller teeth (than fang)		Hollow base extends lengthwise beneath all teeth, and "to a certain height."	Pander's description is so broad that it is difficult to classiiy it under these headings. This is especially true of his description of anterior (?) denticulation.
Ulrich & Bassler, 1926, p. 8, 9		Numerous, their lower half or more sometimes fused but in some cases discrete although crowded.			Ulrich & Bassler made no mention of the general form of the posterior bar, the basal cavity or a lateral process.
Branson & Mehl, 1933, p. 129, 130	Bar- or blade-like. Straight or slightly arched and laterally curved.	Fairly uniform, discrete or, rarely, fused.		Commonly slight excavation on aboral edge at the union of the oral bar and the terminal fang, the upper tip of which is usually flared.	Branson & Mehl regarded the genus as being closely related to *Ozarkodina*. They stressed that forms (which they suggested were intermediate between *Cordylodus* and *Prioniodus*) lacking denticulation of the anticusp may represent a distinct genus, although they represent a complete gradation into species of *Prioniodus*.
Fay, 1952, p. 16			May or may not be present.		This description is included by Fay as part of a key—and cannot therefore be taken as comprehensive.

minutely denticulate. They made no mention, however, of the presence of any lateral process. Branson & Mehl's redefinition of the genus was commonly accepted until the publication of Lindström's (1954) paper.

In a later discussion of the genus (1944, p. 241) Branson & Mehl retained their interpretation of the genus. They discussed at some length, however, material they believed to be from Pander's type locality and formation. Pander in his original description has recorded neither the exact locality nor the formation but stated only "untere silurische Schichten," which means Ordovician. Branson & Mehl recorded the presence of a short, lateral denticulate bar in "typical" specimens. They noted further that the specimens showed a considerable range of variation in form, especially in the lateral process and the denticulation of the anterior edge of the anticusp, both of which were absent in many specimens. They suggested that there was a complete gradation between these and those they regarded as "typical" forms.

Sannemann (1955, p. 151) regarded as belonging to *Prioniodina*, the species excluded from *Prioniodus* by Lindström's redefinition. The type species of this genus is *Prioniodina subcurvata* Ulrich & Bassler. It has a subcentral cusp, a posterior bar and a well developed, denticulated anterior process. Although some atypical species of the genus *Neoprioniodus* have a few denticles in front of the main cusp, these species may, in our opinion, be distinguished from *Prioniodina* by the absence of a *well developed* strongly denticulated anterior process.

THE RESTRICTED INTERPRETATION OF *PRIONIODUS* BY ÖPIK AND LINDSTRÖM

Both Öpik (1936, p. 107) and Lindström (1954, p. 588) suggested that Pander's original description of *Prioniodus* was based upon fragmentary specimens. Both authors also figured material which they claimed to be identical with *P. elegans*. Öpik's material came from the "Glaukonitsand" of Narwa, Estonia, and Lindström's from the "upper and lower Planilimbata limestones" of south-central Sweden.

Pander did not designate the formation, and the type locality of his specimens as well as his type specimens are probably lost (fide Fay, 1952, p. 36). But the "Glaukonitsand" (Grünsand) is one of the Ordovician formations mentioned in the paper of Pander (1856, p. 14). Therefore, it is probable that at least some of Pander's type material was collected from this formation.

Both Öpik and Lindström stressed the "quadraxial" nature of their specimens. Öpik (1936) wrote: "It [the genus] appears quadaxial, with a central cusp and three denticulate wings divergent at unequal angles." Lindström (1954, p. 589) redefined the genus as follows: "Compound conodonts with a subcentral cusp, from the base of which diverge three denticulate edges or processes, one posteriorly, one anteriorly, and one laterally."

If the redefinition is accepted as valid (and the present writers believe that it should be), it will have the effect of excluding from the genus *Prioniodus* the majority of species previously assigned to it. In any case, the genus as redefined by Lindström cannot be regarded as congeneric with the following proposed new genus. The differences between them are considerable and are easily recognized in complete specimens. Since the stratigraphic range of the two genera is different, the division is also of practical value.

THE POSITION OF SOME SPECIES PREVIOUSLY ASSIGNED TO THE GENUS *PRIONIODUS* PANDER

The only method of dealing with the many species of *Prioniodus* which are now excluded from the genus by Lindström's redefinition, appears to be to assign them to a new genus. In spite of Branson & Mehl's (1944) suggestion of a gradation between such forms and those with a lateral process (*Prioniodus* s.s.) in topotype specimens of *P. elegans*, the two broad groups appear to be well differentiated in younger faunas. It will probably be found that *Prioniodus* s.s. is confined to Ordovician strata. At least, no such forms are known to the present writers in strata younger than Ordovician.

The type species of *Dichognathus* Branson & Mehl (1933), *Dichognathus prima*, has a subcentral cusp, from the base of which diverge three edges or processes. It is very

close to *Prioniodus*, from which it is distinguished only by the lack of denticulations on the inner process.

SYSTEMATIC DESCRIPTION

Genus NEOPRIONIODUS, n. gen.

Type-species:—*Prioniodus conjuctus* Gunnell.

Diagnosis.—Compound conodonts consisting of a denticulated posterior bar, at the anterior end of which a large fang (main cusp) is developed. The base of this fang may or may not extend downward below the level of the bar to form an "anticusp," the anterior edge of which may or may not be denticulated. There is usually a basal cavity below the fang, which may be extended as a shallow groove on the aboral surface of the posterior bar.

Discussion.—The typical form of members of the genus consists of a posterior bar with an anterior fang and anticusp which gives rise to the description "pick-like," by a number of authors. The overall structure of the units is generally rather stout and massive, although a few species tend to be more slender.

The anterior fang (main cusp) is frequently more or less massive, with sharp anterior and posterior edges and gently convex lateral faces. Its anterior edge is usually straight but may in some forms be gently convex or concave anteriorly. Its longitudinal axis is straight or gently concave inwards. The fang is bluntly or sharply pointed. The main cusp consists of a single denticle, or it may bear a number of small saw-like denticles along the downward extension of its anterior lower edge. These may be obvious and well developed or present as germ denticles which may be visible only when immersed in oil; in most cases they are completely absent. When present, the denticles tend to be subparallel to the anterior fang. The cusp is often extended below the level of the posterior bar to form an anticusp of variable, and sometimes considerable, length.

If no anticusp is present, in most cases a flaring apron is developed on the base of the main cusp. If denticles are absent, the anterior edge of the anticusp tends to be more or less sharp. The line made by the anticusp and the fang is straight or gently concave anteriorly. The lower terminus of the anticusp may be pointed, blunt or almost spatulate in lateral view. Its posterior lower margin is straight or slightly concave in lateral view. The lower margins may be strongly or weakly flared below the fang on one or both sides or may form an "apron."

The anticusp and fang may be perpendicular to the posterior bar, may make with it an acute angle which is only a little less than a right angle, or may make a somewhat obtuse angle with it.

The posterior bar is straight or gently curved (convex upwards) largely in a vertical plane. It is generally widest at its base where slight marginal flanges may be developed. In some cases it tapers towards the base of the denticles, so that it is broadly subtriangular in cross section. Its length is variable, but commonly approaches or exceeds the combined length of the fang and anticusp. The upper surface of the posterior bar is denticulate, the denticles usually being subparallel to the fang. The denticles may be subequal or may increase in size posteriorly. They are frequently fused but may be completely or largely discrete. At least in "typical" species no second order denticles (inserted in between the bigger ones of first order) are developed. Germ denticles are rare.

The lower surface is commonly excavated by a shallow groove along the posterior bar, which is coalescent with a shallow, subconical cavity below the fang. The groove and basal cavity may in some cases be entirely absent.

Remarks.—Although the holotype of *N. conjunctus* (Gunnell) is fragmentary, many perfect specimens of the species have been collected by one of us (F. H. T. R.), and descriptions and illustrations of other specimens have been published by a number of authors. Ellison (1941, p. 113–114) restudied the type specimens and classed *Prioniodus cacti* and *P.* sp. of Gunnell (1933, p. 267, pl. 32, fig. 32) as junior synonyms of *Prioniodus conjunctus* Gunnell. Youngquist & Downs (1949, p. 169) regarded the latter species as a junior synonym of *P. cacti*, because of the fragmentary character of the holotype of *P. conjunctus*. Since, however, *P. conjunctus* Gunnell (1931) has priority over *P. cacti* Gunnell (1933), it is the trivial

name *cacti* that must be suppressed as a junior synonym.

Stratigraphic range.—The genus appears to range from the Ordovician to the Lower Triassic.

REFERENCES

BRANSON, E. B., & MEHL, M. G., 1933–34, Conodont studies, number 1–4: Univ. Mo. Stud., vol. 8, nos. 1–4, 349 p., 28 pl.

—— & ——, 1944, Conodonts; *in* Index fossils of North America, by Shimer, H. W., & Shrock, R. R.: p. 235–246, pl. 93–94.

ELLISON, S. P., 1941, Revision of Pennsylvanian conodonts: Jour. Paleont., vol. 15, p. 107–143, pl. 20–23, 4 text-fig.

FAY, R. O., 1952, Catalogue of conodonts: Univ. Kansas Paleont., Contr., Vertebrata, art. 3, 206 p. 109 text-fig.

GUNNELL, F. H., 1933, Conodonts and fish remains from the Cherokee, Kansas City, and Wabaunsee groups of Missouri and Kansas: Jour. Paleont., vol. 7, p. 261–297, pl. 31–33.

HINDE, G. J., 1879, On conodonts from the Chazy and Cincinnati group of the Cambro-Silurian, and from the Hamilton and Genesee-shale divisions of the Devonian, in Canada and the United States: Geol. Soc. London, Quart. Jour., vol. 35, p. 351–369, pl. 15–17.

LINDSTRÖM, M., 1954, Conodonts from the lowermost Ordovician strata of south-central Sweden: Geol. Fören. Förhandl., vol. 76, p. 517–604, pl. 1–10, 6 text-fig.

MILLER, S. A., 1889, North American geology and palaeontology for the use of amateurs, students, and scientists: 664 p., 1194 text-fig., Cincinnati, Ohio.

ÖPIK, A., 1936, Konodontidest: On the conodonts Äratrükk Eesti Loodusest, no. 3, p. 105–107, text-fig. 57–59.

PANDER, C. H., 1856, Monographie der fossilen Fische des silurischen Systems der russisch-baltischen Gouvernements: 91 p., 9 pl., St. Petersburg.

RHODES, F. H. T., 1955, Conodont fauna of the Keisley limestone: Geol. Soc. London, Quart. Jour., vol. 111, p. 117–142, pl. 7–10, 6 text-fig.

SANNEMANN, D., 1955, Oberdevonische Conodonten (to IIα): Senckenbergiana lethaea, vol. 36, p. 123–156, pl. 1–6, 4 text-fig.

SWEET, W. C., 1955, Conodonts from the Harding formation (Middle Ordovician) of Colorado: Jour. Paleont., vol. 29, p. 226–262, pl. 27–29, 17 text-fig.

ULRICH, E. O., & BASSLER, R. S., 1926, A classification of the toothlike fossils, conodonts, with descriptions of American Devonian and Mississippian species: U. S. Nat. Mus. Proc., vol. 68, p. 1–63, 11 pl., 5 text-fig.

YOUNGQUIST, W., & DOWNS, R. H., 1949, Additional conodonts from the Pennsylvanian of Iowa: Jour. Paleont., vol. 23, p. 161–171, pl. 30–31.

MANUSCRIPT RECEIVED DECEMBER 8, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 700–706, 1 TEXT-FIG., MAY 1956

SOME PARADOXES IN TAXONOMY WITH REFERENCE TO THE PROTISTA

ROUSSEAU H. FLOWER
New Mexico Institute of Mining and Technology, Socorro

ABSTRACT—Evolution is a process of gradual and sometimes devious changes. Specializations in any large group may depart from the definitions which we have set up for recognition of the group in general. Where there are no transitions between major groups, relationships are inferrential or uncertain; where they are known, the taxonomist sometimes challenges the distinctness of the groups. These paradoxes result from the classification of organisms into discrete departments, when in reality evolution produced gradual change. Some extreme modifications are placed phyletically only on the basis of relationships shown in restricted ontogenetic stages; omission of these stages is possible, and may well account for some small groups of seemingly isolated position. Emphasis is placed upon morphological simplification accompanying tiny size, parasitism, or both.

It has been recognized since the days of Haeckel, that the plant-animal distinction is a mere fiction when applied to primitive organisms. The use of the Protista for such forms in the Treatise of Invertebrate Paleontology, is a formal taxonomic expression of a long recognized reality, and serves to avoid essentially artificial procedural difficulties. Recent criticisms of the procedure do not appear to be valid.

The relationships of primitive organisms are reviewed. It is evident that the plant-animal transition occurs several times, and is phyletic in the Mastigophora, probably homeomorphic elsewhere. Though the use of Protista presents some anomalies—as will any major group—it should be welcomed as a taxonomic recognition of real relationships which have long been generally accepted.

INTRODUCTION

Our present classification of organisms is based upon an arbitrary and unnatural concept of discrete units, of compartments distinct from one another, each divisible into further compartments down to the species and subspecies. It was developed prior to the realization of organic evolution. We have subsequently come to recognize that evolution, being the devious process that it is, presents countless anomalies which become greater as larger and larger units are surveyed. The larger the group, the greater is the probability that within it somewhere one will find exceptions to the short succinct definition by which (we are generally taught) that group is distinguished from others. It is not surprising that this is true; it would be more surprising were it not. The anomalies thus presented are numerous and have sometimes led to some amusing incidents. One key to the orders of insects was published in which a wingless gallwasp would key out into the fleas. Paedogenesis, if it became a universal feature of any one group of insects, would eliminate the adult stages by which its hexapod relationship is evident, and might even tend to obscure the affinities of such a small group as the Strepsiptera with the insects. In the Arthropoda the Tardigrada and Pentastomida are so modified that their arthropod nature is not evident from casual inspection; some pentastomids rather resemble tapeworms. The remarkable degeneration of the adult of the Rhizocephala of the Cirripedia leaves the cirripede and indeed the arthropod affinities evident from the young stages rather than from the adult. The anomalous Mesozoa, simple and exclusively parasitic organisms, may well be developed from some Metazoan group so degenerate morphologically, because of their parasitic habit, that all vestiges of their true origin have been lost. Tiny size causes extreme simplification in some organisms; a rotifer may have a digestive track composed of only five or six cells. One may speculate that further simplification might produce organisms in which the cell boundaries are lost. It is intriguing to contemplate that such simplification might account for some of the complex polynucleate parasitic ciliate protozoa. Thus

surely, it must be recognized that in the devious processes of evolution the evidence of bizarre specialization, including degeneracy of structure which is a specialization in itself, suggests strongly that some of the small anomlous groups might have developed as deviations from others more complex morphologically, but that all evidence of the relationship might be lost. We must place those forms as well as we can from the evidence that is available. The greatest problem in taxonomy is the tracing of relationship; the distinction between phyletic relationship and homeomorphy is sometimes the most difficult to demonstrate.

It has been recognized quite universally for many years that dogmatic definitions cannot serve to distinguish discrete compartments; there will be intergradations where there are relationships. If they are not always apparent to the neontologist, it may be that the transitional forms died out, and the living forms present no transitional features. If they are not apparent from the paleontological record, it may be because the transitional organisms left no preservable remains. The paradox in taxonomy remains as this: if no transitional forms are known between two major groups, their relationships cannot be proved and arguments may develop. If transitional forms exist, someone is sure to raise the criticism that the groups are not distinct because they intergrade. Either way, you lose.

It has long been recognized that the most widely and popularly known distinction among organisms, between plants and animals, fails completely when the most primitive organisms are considered. True, the division Protista does not appear in textbooks widely. True, we divide those who study organisms into zoologists and botanists, or, sometimes, animal and plant biologists, under the impression that under these terms their viewpoints may somehow become broader and more philosophical. We have departments, and societies under these categories. But the workers in both fields have recognized since at least the time of Ernst Haeckel that there are living today many simple organisms which are not properly plant or animal. There is a no-man's-ground there which is accepted as a proper field for investigation by botanists and zoologists alike; this overlap has been amicably accepted for many years; it has been recognized that here dispute as to the plant or animal nature of these forms is a futile procedure and a waste of time. If life had a common origin, it must be expected that such creatures must have existed in the past. We are doubly fortunate that, fundamentally soft-bodied as such creature were, we have multitudes of them alive today, available for study.

Moore (1954) has cut the gordian knot of the treatment of these primitive forms, many of which develop preservable hard parts which are retained in the fossil record, by employing the term Protista. The formal appearance of this name effectively unites these primitive generalized organisms, and should be widely welcomed, particularly by those of us who are less informed on neontology, as a step away from a distinction of all organisms into plants and animals, a division which has long been recognized here as one of the fictions to which our classifications still cling. It is indeed, not unlike the old game in which one may presumably divide the animal kingdom into "fish, flesh and fowl." Amazingly, however, Weller (1955) has seen fit to object to this procedure. Strangely, Weller has previously written other papers insisting that the paleotologist should be a geologist, and it is apparently true that there are many in the field whose knowledge of geological matters is intimate, and whose familiarity with biological thought is somewhat tenuous. I once overheard a lecture in elementary paleontology in which the class was informed that the Protozoa were divided into the Foraminifera and Radiolaria. The Protozoa, of course, are divided into the Sarcodina, Mastigophora, Sporozoa and Ciliata, and the Foraminifera and Radiolaria are only two minor divisions (among eight others) of the Sarcodina, the hard parts of which happen to be fairly abundant in sedimentary rocks. If this is a fair sample of paleontological teaching, it is fitting that in a paleontological journal some notice should be taken of these criticisms.

Objections are discussed under matters of (1) convenience, (2) philosophic and (3) practical considerations. Under convenience

it is stated that though specialists might favor the use of the Protista, yet they are unlikely to take an objective view of the taxonomic system as a whole. One can hardly take seriously the implication that those who have studied closely the point at which the former plant and animal kingdoms merge are not best informed upon these matters, and possibly that their knowledge of organisms is not as confined to such groups as this conclusion would imply. Quite possibly these informed "specialists" are more competent to pass on this matter. It is suggested that while uniformity of classification might be achieved, the same result might be obtained by agreement. It is doubtful whether students of living things will be more or less inclined to agree on the rank to be given a particular group, or its exact scope or relationship, whether the present Protista are placed in a kingdom by themselves or divided up between plants and animals, a matter which has not, as I have said before, been taken very seriously.

Under philosophic considerations the arguments may be discussed as follows:

A. It is true that recognition of a protistid kingdom implies that the distinction of this group from plants and animals respectively is more important than the distinction between plants and animals "as commonly recognized." Neontologists have long recognized that the dichotomous division of organisms at this level is a matter of fiction rather than fact. It is therefore high time that this was expressed in classification. To insist that plant-animal distinctions are more important must be admittedly subjective, and a matter which may loom larger in the minds of those unfamiliar with lower organisms than those who are familiar with them. Rather than obscuring "the most fundamental of all distinctions in the organic world" the use of the Protista reflects one of the greatest truths: the unified origin of all organic life.

B. The assertion that a "horizontal" is less natural than a "vertical" classification is a matter of opinion on which no unanimous support can be expected.

Three points are raised under practical considerations:

A. Recognition of the Protista required restriction and redefinition of the animal kingdom. This is true, but rather pointless as the boundary has been long recognized as gradational by biologists. Indeed, it has been found that here the distinction between plant and animal is neither useful nor significant.

B. The protistid kingdom will not eliminate overlap of interest by zoologists and botanists. This is true, but hardly a valid point. Distinctions of biologists into zoologists and botanists is academic, administrative and historical. Whether a third kingdom is justified or not, one cannot expect the amalgamation of departments, courses, societies, or all other equippage built up about academic and secientific procedures.

C. The protistid kingdom does not solve the problem of intermediate forms, Why should one expect it to do so? The accompanying diagram and summary of the primitive groups will show something of the true situation. It is debatable whether the argument there presented that sponges as well as higher algae should be included in the Protista is valid, or even particularly relevant.

D–E. It is stated that recognition of the Protista encourages the recognition of one or more additional kingdoms, and the erection of more phyla. That either procedure would be necessarily evil in itself is implied, but why it should be viewed in this light is not made clear. There is certainly much to be said for the segregation of the more primitive forms without definite nuclei, the Moneres, whether as a separate kingdom, subkingdom, or superphylum, is a matter of secondary importance.

F. A new code of international rules of nomenclature might, as suggested, be required for the Protista. It is, however, equally conceivable that that established either for animals or plants could be extended. In either case, the question is not a suitable basis for arguing the validity of the kingdom. That it is brought up is a reflection of the fact that many paleontologists are overconcerned with matters of nomenclature. Sinclair (1953) had occasion to remark in another connection that after all, paleontology is the study of fossils, and not of the names of fossils.

SURVEY OF PRIMITIVE ORGANISMS

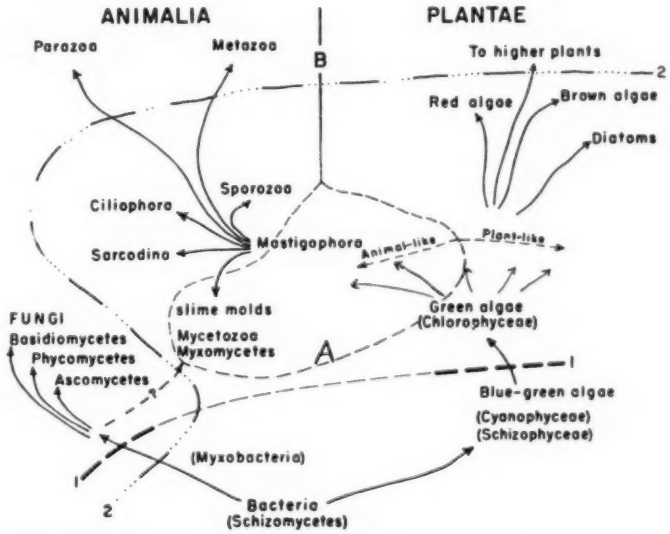
If one surveys what is known, and the concepts rather widely held about primitive organisms, it becomes evident that while several solutions are possible, there is much to be said for the recognition of the Protista.

The accompanying diagram (Text-fig. 1) will show something of the evolution of the more primitive forms of life, and indicates at the same time the overlapping of botanical and zoological interest. This overlap occurs because the division between two kingdoms, plant and animal, breaks down to an extent that it has no reality. That the recognition of a third kingdom, Protista presents some anomalies is obvious; it serves to express, however, the acellular nature of the primitive organisms it contains, their unity in a group in which the plant-animal distinction has long ago been dismissed by neontologists as profitless busy-work.

The nomenclature of major groups has been greatly simplified, largely to keep the diagram from being overloaded with complexities which might make the fundamental situation less graphic.

Bacteria.—The Bacteria, the Schizomycetes, are simple cells without proper nuclei. They lack the specialized chemicals by which the higher Cyanophyceae can perform photosynthesis. The most familiar bacteria are those which require organic food, and are saprophytic or parasitic, but there are others which can manufacture their food from inorganic substances. Physiologically, such organisms are potentially primitive, for the first life forms must of necessity have lived on inorganic substances.

Much has been written concerning the filtrable viri. They lack structure, other than the chemical structure of their molecules. Morphologically they fulfill the ideal requirements for the primitive life forms.



TEXT-FIG. *1*—Generalized diagram of relationships among primitive organisms. Line 1 marks the division between the primitive forms without well delimited nuclei, the Moneres of Haeckel, and higher organisms with definitie well defined nuclei. The solid line B represents the division between the higher Animalia and Plantae. It descends to the broken line A which embraces those forms so intermediate that they have been considered as both plants and animals. There is overlap, in the nearly synonymous Mastigophora and Chlorophyceae, and again in the Mycetozoa. Line 2 indicates the proposed division between the Protista, the Plantae and Animalia. It is evident that the only serious objection lies in the grouping of the fungi with the Plantae. The great overlap in the old plant-animal division occurs in the largely overlapping simple green algae and the flagellate Protozoa, and again in the slime molds. Probably the slime-molds are specialized Protozoa which are homeomorphic with the true fungi.

However, no viri seem to be known which are not dependent on other organic substances, and usually directly on other organisms. Therefore they are specialized physiologically and unconvincing candidates as the first life-forms. Indeed, they could be interpreted as morphologically degenerate bacteria.

One extremely interesting group, the Myxobacteria, appears to be intermediate in some respects between the true bacteria and the simpler molds, and complicates the distinction between bacteria and simple fungi.

Blue-green algae.—The blue-green algae, the Cyanophyceae or Schizophyceae, show a structural simplicity which allies them with the preceding group, but they are advanced in the possession of specialized substances, often both chlorophyll and phycocyanin, by which they can manufacture their own food by photosynthesis. Together with the bacteria, they constitute the primitive Moneres, proposed by Haeckel as a subkingdom.

Green algae.—The green algae, the Chlorophyceae or Chlorophycophyta, show a much more complex structure and a definite nucleus. Primitively, they have chlorophyll and are capable of photosynthesis. They range from simple solitary cells, usually equipped with one or more flagella, to solitary or colonial forms with a rigid cell wall. Colonies range from simple aggregates, through slender unbranched filaments (the mesh-like *Hydrodictyon*), through globular or irregular clusters, to ramose colonies, which become gradually larger and more obviously plant-like in aspect, and include among the more specialized forms some seaweeds and specialized fresh-water forms such as *Chara* and its allies.

It is among the solitary flagellate forms that there is a complete gradation into the Mastigophora of the Protozoa. Some such forms may feed either by photosynthesis, or by engulfing food particles. Some form complex colonies, like the sphaeroidal colonies of *Volvox*; other colonies are irregular, dendritic or radial. Some forms build tests of silica and other substances, notably the remarkable Dinoflagellata. The Choanoflagellata with a collar around the flagellum, are the probable origin of the Porifera, and possibly of the Animalia as a whole.

Higher algae.—Several distinct plant-like groups stem from the green algae. The diatoms, solitary forms without green coloring, are now generally considered as a separate group, the Chrysophyceae. The brown algae, the Phycophyceae or Phycophycophyta and the red algae, the Rhodophyceae or Rhodophycophyta, are sedentary obviously plant-like forms embracing most of the seaweeds, and sometimes attaining immense size. It is the blue-green, green, brown and red algae which, a generation ago, were united in the Thallophyta.

Fungi.—The fungi as a group are differentiated from the bacteria primarily by the development of more complex cell structure and, in particular, the development of a good nucleus. The change parallels, but is independent of, that found between the blue-green and the green algae. The three main groups of fungi are indicated in the accompanying figure and need not be discussed in detail. The main part, the mycelium, consists of a meshwork of generalized cells. It is the reproductive portion producing spores, which becomes immensely specialized in the higher forms and, being an immobile plant-like growth, is responsible for the inclusion of fungi in the plants. Yet their only link with the higher plants is through the archaic Schizomycetes. The group lacks ability to manufacture its food and must live upon organic matter, dead or living.

Mastigophora.—Zoologists have included the flagellate Protista among the Protozoa, while most of the same forms have been included by botanists among the Chlorophyceae. True, in the green algae there are forms, ranging from solitary ones to those forming complex colonies, which the zoologist has never claimed, but it is among the simpler forms, lacking cell walls, that the animal-plant distinction is clearly a fiction. Among such forms are all degrees of complexity of morphology, degrees from solitary through simple to complex colonies. Some are dominantly autophytic, manufacturing their food by chlorophyll, others feed dominantly by ingesting food, a good many can do both.

The Mastigophora are probably the primitive radicle from which other divisions of the "Protozoa" were derived, for here and there in other members of the group, in forms which can be convincingly accepted as primitive, a flagellum appears. The digestive epithelium of the Porifera as already noted, consists of collared flagellated cells. That of the Coelenterata, the simplest of the Metazoa, is again of flagellated cells. Though flagella are absent in the digestive epithelium of most higher animals, they are still retained in the motile element of the reproductive stage, the sperm. It is in discussing this group that the Protista serves its greatest nomenclatorial need, for it is an eternal vexation to refer to its members as either plants or animals.

Several groups of the Mastigophora left unclaimed by botanists include those forms, sometimes quite complex structurally, which are either symbiotes or internal parasites. Some, such as *Giardia* which inhabits the alimentary track of the Isoptera, and digests cellulose for it, are symbiotes necessary for the life of their host. Others as the Trypanosomes, are responsible for some interesting diseases.[1]

Sarcodina.—Here are placed the "Protozoa" which move and feed dominantly by pseudopodia. The presence of flagella in a few forms suggests an origin in the Mastigophora. Many of the free living forms secrete tests and skeletons, some attaining remarkable complexity. A few forms are parasitic.

Ciliophora.—These are the ciliate "Protozoa," most free living, some parasitic. Structurally, this group contains the most complex of the forms, ranging from complex polynucleate parasitic forms, to the free-living hypotrichs, which crawl with fused cilia, and move around on patches of debris like so many little beetles. Here again are a number of forms which secrete hard tests. Occasional flagella here suggest an origin in the Mastigophora.

Sporozoa.—These are simple parasitic forms in which spore formation is a conspicuous part of their reproductive cycle. Again, occasional flagella suggest an origin in the Mastigophora.

Mycetozoa-Myxomycetes.—These are the slime molds, which appear sometimes as motile masses of protoplasm, with pseudopodia and flagella suggesting a connection with the primitive Sarcodina and ultimately with the Mastigophora. A possible connection with the Rhizopoda is suggested by *Chlamydomyxa* and *Labyrinthula*. Yet reproductive stages in which spores are produced, are so similar to those of the molds that these same creatures are included by botanists with the fungi and called the Myxomycetes. The flagellum suggests that these forms are aberrant "Protozoa" adapted for life outside of a liquid environment, rather than fungi which approach animals in motility.

ANIMALIA

The primitive nature of sponges has long been recognized, which is expressed by their segregation into the Parazoa, apart from the Metazoa and Protozoa of the old classification of animals. The division of the Metazoa into Agnostozoa, including only the parasitic Mesozoa, and the Metazoa, including all higher animals is a useful expression of the factual situation. The procedure, however, could be taken to imply an origin of the Mesozoa from the Protista independent of the Parazoa or Metazoa. Such an interpretation the writer regards as unlikely. Rather, it seems that the Mesozoa may be highly degenerate forms derived from higher Metazoa, but so simplified that their morphology and ontogeny not longer retain any clue as to their precise origin.

PLANTAE

No questions arise concerning the higher plants in general, characterized by alteration of gametophyte and sporophyte generations. The criticisms that the higher algae should be excluded from the Protista seem to stem from those who feel that they are obvi-

[1] It is perhaps not out of line, in view of those who would cling to a fictitious plant-animal distinction to point out, as I did to one nurse who was very superior about the matter, that there are no such things as germs. Some diseases are caused by viri, others by bacteria, others by protozoa, fungi, and some Metazoa. When all diseases are sorted out, there are no organisms left over; therefore there are no germs. I never saw this particular nurse again. Possibly the argument so confused her that she left the profession.

ously plants, and sometimes big ones, but organization and reproduction are such that those esoteric specialists who really know something about them would group them with the Protista rather than the plants if the Protista as a group is to be recognized at all.

SUMMARY

The Protista is a convenient and significant receptacle for primitive organisms which are properly neither plant nor animal. Its use involves some paradoxes, but they are somewhat less, perhaps, than those involved in a rigid dichotomous division of living things into two kingdoms. Where two kingdoms are recognized, it must be admitted that animals sprang from plants at the shadowy border where the green algae and the flagellate protozoa merge and overlap. A second overlap occurs in the slime-molds, but is perhaps a specialization from the "Protozoa" adapted to a non-aquatic environment, rather than a true link with the fungi. Should the intriguing possibility ever be demonstrated that among the more structurally complex parasitic protozoa, there were included highly degenerate forms of metazoan origin, they might be removed from the Protista, but this would be no suitable argument against the validity of the group. Weller expresses the opinion that once the Protista are generally recognized the proposal of still other kingdoms might be in the offing. A glance at the accompanying figure will show that the fungi occupy a position isolated from the Plantae as a whole, and the erection of a separate kingdom for their reception, or else their inclusion in the Protista, would be a suitable taxonomic expression of an evolutionary pattern which has been recognized by botanists for better than a generation.

Probably the greatest contribution made by the recognition of the Protista is taxonomic recognition of the long-evident fact that the plant-animal distinction is a fiction in simpler organisms. If it comes as a shock to those who were oblivious of this situation, their consternation is not unlike that with which a believer in a flat earth would view a diagram of the galaxies.

Paradoxically, the old dichotomous plant-animal division works well only when employed by those who realize its inherent weakness and refuse to be concerned over the nomenclatorial, academic, and procedural difficulties which they might otherwise bring down upon themselves. Yet it seems to be those who are completely unaware as to how fictional the division is who are sure to protest its formal abandonment.

REFERENCES

MOORE, R. C., 1954, Kingdom of organisms named Protista: Jour. Paleont., vol. 28, p. 588–598.

SINCLAIR, G. W., 1953, Notes on forensic paleontology: Jour. Paleont., vol. 27, p. 608–609.

WELLER, J. M., 1955, Protista: non-plants, non-animals? Jour. Paleont., vol. 29, p. 707–710.

MANUSCRIPT RECEIVED AUGUST 28, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 707–711, 1 TEXT-FIG., MAY 1956

THE OCCURRENCE OF PALEOCENE MAMMALIAN REMAINS IN THE FOSSIL BASIN OF SOUTHWESTERN WYOMING[1]

C. LEWIS GAZIN
U. S. National Museum, Washington, D. C.

ABSTRACT—A fauna of Tiffanian, upper Paleocene age is recognized in a collection of rather fragmentary mammalian remains discovered in the Fossil Basin, southwestern Wyoming, about three miles east of Fossil station on the Union Pacific Railroad. The exposures are of essentially light gray sandy clay, possibly of the Evanston formation, apparently unconformable beneath the variegated Knight formation of Eocene age. The Knight in this area is in turn capped by the Green River formation with its well known fossil fish quarries. A large proportion of the Paleocene mammal remains obtained are isolated teeth of the primate *Plesiadapis*, tentatively regarded as the species *P. fodinatus* Jepsen, originally described from the Silver Coulee horizon of the Polecat Bench formation in the Big Horn Basin.

INTRODUCTION

DISCOVERY of the occurrence of fossil mammalian remains of Paleocene age in the Fossil Basin of southwestern Wyoming can scarcely be regarded as unexpected with two formations of this age, the Evanston and Almy, included in the stratigraphic sequence of the basin. It is, on the other hand, perhaps surprising that the discovery was not made much earlier, considering the ready accessibility of the exposures and their proximity to the intensively worked fossil fish quarries of the Green River formation.

The locality in question is about 3 miles east of Fossil Station on the Union Pacific Railroad in Lincoln County, Wyoming, very near the quarter corner on the line between sections 11 and 14, T. 21 N., R. 117 W. The exposures are visible from the highway, U. S. 30N, and extend for about a mile east and west on the south side of the railroad tracks. They form the spur separating the East Fork of Twin Creek from the main or south fork near their junction.

The formation represented is not certainly identified but may possibly be a part of the Evanston. It certainly does not resemble the type Almy in the vicinity of Evanston, or exposures recognized as Almy along the western margin of the upper Green River basin to the north. The beds are essentially a gray, sandy clay lightly streaked with yellowish buff and with scarce, highly localized reddish zones, as at the fossil locality. The beds were early regarded as belonging to the lower part of the Knight formation, but the relationship between the two is surely unconformable[2] as the Paleocene has a distinctly greater southerly dip than the overlying Knight. Evidently the same formation, but including some highly carbonaceous layers, has been recognized beneath the Knight about 16 miles to the west-southwest, in the basin west of Elk Mountain, in vicinity of the quarter section corner between sections 8 and 17, T. 20 N., R. 119 W. On the other hand, the comparatively light colored beds around the base of nearby Fossil Butte, however, are not the same, as *Hyracotherium* has been found in the lowest of these exposures.

The first determinable specimen from the Paleocene near Fossil Station was a *Phenacodus* jaw found by Dr. D. H. Dunkle in 1950 during his investigation of the nearby Green River fish occurrences. The specimen was described (Gazin, 1952, p. 6, 8, 10, 61) as coming from, "gray exposures beneath the red beds," at that time regarded as a part of the Knight formation. Remains definitive of a Paleocene age were discovered by F. L. Pearce while carrying on field work with me in 1953 but it was not until the collections were unpacked in the laboratory

[1] Published by permission of the Secretary of the Smithsonian Institution.

[2] The geologic relations in the region are currently under study by W. W. Rubey and J. I. Tracey of the U. S. Geological Survey.

that their age significance was recognized. The locality was revisited in 1954 and the rather limited productive area, which consists of an outwash apron perhaps 50 feet across on the west side of a low spur of badlands, was rather thoroughly covered.

The material is very fragmentary, consisting mostly of isolated teeth, with only a few jaw portions exhibiting as many as two or three teeth. The fauna recognized is as follows with the approximate number of specimens representative of each indicated so that some clue may be had as to the complexion of the fauna:

Ptilodontid, possibly *Ptilodus* sp.	1
Plesiadapis cf. *P. fodinatus* Jepsen	56
Thryptacodon cf. *T. australis* Simpson	11
Claenodon near *C. ferox* (Cope)	2
Arctocyonid creodont	1
Didymictis? sp.	1
Litomylus? ishami, n. sp.	1
Haplaletes, possibly *H. pelicatus* Gazin	1
Gidleyina? near *G. wyomingensis* Gazin	3
Phenacodus sp.	8
Pantodont? undet.	2

There would appear to be little doubt but that the foregoing assemblage is Tiffanian in age, probably not as early as the lower and faunally better represented of the horizons in the Bison Basin sequence, or as early as the Melville, but more nearly equivalent to the Silver Coulee horizon of the Polecat Bench sequence.

Evidence for a Tiffanian age is seen largely in the association of forms. Moreover, although the representation is meager and highly fragmentary in nature, apparently significant information may be derived from the developmental stage or species suggested in certain of the genera. In this instance, the better represented materials of the post-Torrejonian genera, *Plesiadapis* and *Thryptacodon*, in general appear to be of Tiffanian species, not however indicative of the earliest Tiffanian, to judge from the Bison Basin sequence. Supporting evidence seems forthcoming from the *Phenacodus* materials. The *Phenacodus* is distinctly more progressive in the direction of *P. primaevus* than the more *Tetraclaenodon*-like *P. bisonensis*.

Forms having comparatively early affinities would include the ptilodont, *Didymictis?*, *Litomylus?* and *Haplaletes*. The ptilodont corresponds closely only to the Crazy Mountain Torrejonian *Ptilodus montanus*, but the specimen is truly inadequate for even generic reference. Moreover, so far as the relatively early age implied by the possible presence of *Ptilodus* is concerned, a small species believed to be of this genus, *P? fractus* Dorr, is known in the Dell Creek Tiffanian of the Hoback Basin. The *Didymictis* represented cannot be distinguished from Torrejonian *D. haydenianus*, but here again the material is inadequate, although the later *D. protenus* and Tiffanian *D. dellensis* are clearly not indicated. *Litomylus?*, while suggestive of Torrejonian or early Tiffanian, is represented by a species of rather unusual size, so that recognition in it of an advanced stage may not be illogical. The *Haplaletes* is close in size to the early Tiffanian *H. pelicatus* but this genus is represented by *H. serior* in the highest of the Bison Basin levels so that the genus evidently did not disappear in comparatively early Tiffanian time.

Included in the following annotated listing of the Mammalia is the description of a new condylarth species.

ANNOTATED LIST OF MAMMALIA

Order MULTITUBERCULATA

Family PTILODONTIDAE

Ptilodontid, possibly PTILODUS, sp.

A single multituberculate specimen, a little more than half of a right P_4, is included in the collection. The tooth can be closely matched in size, profile and ridges with *Ptilodus montanus* from the Gidley quarry in the Crazy Mountain Fort Union. The anterior margin of the tooth is similarly notched, but shows much less evidence of a longitudinal groove on the anterior root for the position of P_3. This might indicate the absence of a P_3 in the form represented, such as noted in certain material of *Ectypodus*, particularly the later species. However, the Twin Creek P_4 is much larger than in any species of *Ectypodus* and shows separate and parallel anterior ridges, not bifurcating as defined for *Ectypodus* (Jepsen, 1940, p. 264). The profile of the tooth is quite unlike that of *Anconodon*.

Order PRIMATES

Family PLESIADAPIDAE

PLESIADAPIS cf. P. FODINATUS Jepsen

Teeth of *Plesiadapis* comprise in number about two-thirds of the entire collection.

These correspond most closely to those in *Plesiadapis fodinatus* Jepsen from the Tiffanian horizon of the Polecat Bench series in the Big Horn Basin. For example, the average for the length of M_2 is only about 0.1 millimeter less than in the type of *P. fodinatus*. The width of M_2 is likewise close. On the other hand, the various third lower molars though not so numerous are noticeably smaller. M^3 may also be a little smaller than in referred material of *P. fodinatus* from the Silver Coulee. The lower molars are distinctly wider than in *Plesiadapis rubeyi* of the Almy and generally larger than *Plesiadapis dubius* of the Clark Fork. The form represented by the material from the forks of Twin Creek is, nevertheless, allied to these species and *P. gidleyi* rather than the group exhibiting the more sloping labial cusps in the lower teeth, which includes *P. rex*, *P. anceps*, and *P. jepseni*.

Order CARNIVORA
Family ARCTOCYONIDAE
THRYPTACODON cf. T. AUSTRALIS Simpson

Of the 11 specimens representing *Thryptacodon*, nine would appear to represent *T. australis*: The best of these, a jaw portion with M_3 and most of M_2 (USNM No. 21261) differs by less than a tenth of a millimeter in dimensions given by Simpson (1935b) for these teeth in the type. It likewise exhibits the well separated hypoconulid in M_3 noted in the type. Two or three isolated first lower molars are a little larger than in the type but also probably belong to the same species.

Two distinctly small specimens of *Thryptacodon*, a jaw portion (USNM 21260) with M_3 and part of M_1 and an isolated upper molar, may be from no more than a variant of *T. australis* but possibly, as interpreted in the case of the Bison Basin faunas, represents a distinct species. The third molar in USNM 21260, is scarcely more than 12 per cent shorter and 10 per cent narrower than in USNM 21261 above, tentatively referred to *T. australis*. Simpson (1937b) noted that there are two groups based on size range in the Sand Coulee and Gray Bull materials, with the possibility not proven, that the smaller of these characterized the Sand Coulee. He regarded the two groups as possibly subspecies of *Thryptacodon antiquus*. The differences here are of about the same relative magnitude so that no more than a subspecific difference might likewise be interpreted for the Twin Creek material.

CLAENODON near C. FEROX (Cope)

A left ramus of the mandible (USNM 21259) with M_1 and M_3 and an isolated upper molar show no characters by which they may be distinguished from Torrejonian material of *Claenodon ferox*. The size of the teeth is near that of typical *Claenodon corrugatus*, which Simpson (1937a) has shown to be a synonym of *C. ferox*. *Claenodon* is now known to occur in Tiffanian (Bison Basin) and Clarkforkian (Almy) as well as Torrejonian horizons with an apparent descendant *Anacodon* in the lower Eocene.

Arctocyonid creodont

A jaw fragment with M_1 and the posterior margin of P_4 may well be from an oxyclaenine arctocyonid. It is near *Tricentes subtrigonus* in size but M_1 is relatively longer and more slender. The protoconid and metaconid are closer together and the small paraconid is low, median and much more anterior in position. The elongation of the molar gives somewhat the impression of a triisodont type, but the trigonid is much less elevated.

Family MIACIDAE
DIDYMICTIS? sp.

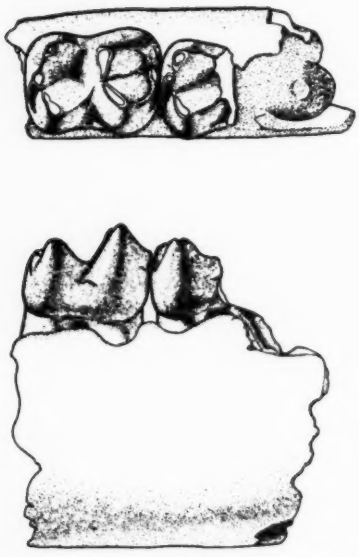
Didymictis is indicated by only the talonid portion of an M_1. The species cannot be determined but in size of carnassial it is only a trifle smaller than Torrejonian *Didymictis haydenianus*, much smaller than any of the subspecies of *D. protenus* in the Clark Fork or lower Eocene, or than *D. dellensis* from the Hoback Basin. On the other hand, the Twin Forks tooth is clearly from a species larger than *Didymictis microlestes* or *D. tenuis* of the Crazy Mountain Fort Union.

Order CONDYLARTHRA
Family HYOPSODONTIDAE
LITOMYLUS? ISHAMI,[1] n. sp.

Holotype.—Right ramus of mandible with M_2 and talonid of M_1. USNM, 21263.

Horizon and locality.—Twin Creek Forks Paleocene, NE corner of NW¼, section 14,

[1] Named for Mr. Lawrence B. Isham, scientific illustrator in Department of Geology, U. S. National Museum.



TEXT-FIG. *1*—*Litomylus? ishami*, n. sp. Portion of right ramus of mandible with M_2 and talonid of M_1 (USNM 21263), occlusal and lateral views, ×4. Paleocene, Evanston? formation, near Fossil, Wyoming.

T. 21 N., R. 117 W., Fossil Basin, Lincoln County, Wyoming.

Specific characters.—Size of anterior lower molars about 30 per cent greater than *Litomylus dissentaneus* Simpson and nearly 20 per cent greater than *Litomylus scaphicus* Gazin. Trigonid of M_2 a little more inflated appearing and paraconid slightly more reduced than in *L. dissentaneus*. Hypoconulid on M_1 relatively a little closer to the entoconid.

Discussion.—One may well be censured for defining a species on material which would seem so nearly inadequate as in this case. Nevertheless, the complete lower molar in the type specimen is in a perfect state of preservation and scarcely worn so that its relationships should be determinable. Moreover, the second molar and incomplete first are so strikingly like those in the much smaller genotypic species, *Litomylus dissentaneus*, that one scarcely hesitates in drawing attention to the comparatively large species represented. Doubt is attached to the generic reference only because the character of P_4 and, to a certain extent, that of M_3 are not known and these teeth are rather significant in the diagnosis of *Litomylus*. M_2 in *L. ishami*, however, even more closely resembles that in *L. dissentaneus* than does this tooth in the intermediate size, *Litomylus scaphicus*.

HAPLALETES, possibly H. PELICATUS Gazin

A single upper molar tooth almost identical in form to the very much smaller M^3 in the paratype upper dentition of *Haplaletes disceptatrix* Simpson (1937a) may possibly be of *Haplaletes pelicatus*. *H. pelicatus* is the smaller of the two comparatively large species of this genus occurring in the Bison Basin faunas and comes from the lowest level discovered or that at the so-called saddle locality. Upper teeth of *Haplaletes* were not discovered in the Bison Basin collections but the Twin Creek molar would appear to be between *H. pelicatus* and the stratigraphically higher *H. serior* in size, perhaps a little closer to *H. pelicatus*.

GIDLEYINA? near G. WYOMINGENSIS Gazin

Of the three specimens believed to be of *Gidleyina*, two are isolated teeth and the third (USNM 21264) is comprised of portions of both rami of the mandible with Dp_2-M_2 represented, together with an associated upper molar. USNM 21264, though scrappy, is clearly the best specimen in the Twin Creek Forks collection. No premolars, upper or lower, are represented so that reference to *Gidleyina* rather than *Ectocion* is rather dubious. Nevertheless, the upper molar belonging to USNM 21264 shows anteroexternal and posteroexternal crests from the protocone joining the protoconule and metaconule respectively rather prominently as in *Gidleyina*. Moreover, the hypocone is well separated from the metaconule, with no suggestion of the posterior loph which tends to develop between these cusps in *Ectocion*.

There is no certainty that the form represented is *Gidleyina wyomingensis* but the size of teeth is very close and no significant differences were noted.

PHENACODUS sp.

There are eight specimens of *Phenacodus* and three of these are lower jaw portions or lower teeth that cannot be distinguished from *Phenacodus primaevus*. One of these, USNM 21265, exhibiting well worn P_4 and

M_1 was earlier cited (Gazin, 1952, p. 6, 8, 10, 61) as representing *P. primaevus*. The upper molars, however, where not too well worn show that the metaconule though weak was not so posteriorly placed, being about in line with metacone and hypocone. Moreover, these teeth as in *Phenacodus grangeri* are transversely broad and not so rounded as they are in *P. primaevus*. The Twin Creek Forks teeth, including both upper and lower, are all larger, however, than in the *Phenacodus grangeri* type and paratypes from the Tiffany beds.

Order PANTODONTA
Pantodont? undet.

A number of small fragments of comparatively large upper cheek teeth, evidently from two different individuals, seem almost certainly to be pantodont; several of these can be closely matched with tooth portions in known pantodont material. It seems clearly evident, moreover, that certain of these cannot be Uintathere tooth structures, so that *Probathyopis* is not represented.

REFERENCES

DORR, J. A., JR., 1952, Early Cenozoic stratigraphy and vertebrate paleontology of the Hoback Basin, Wyoming: Geol. Soc. Am., Bull., vol. 63, p. 59–94, 6 fig., 7 pl.

GAZIN, C. L., 1942, Fossil Mammalia from the Almy formation in western Wyoming: Washington Acad. Sci., Jour., vol. 32, no. 7, p. 217–220, 2 fig.

——, 1952, The lower Eocene Knight formation of western Wyoming and its mammalian faunas: Smithsonian Misc. Coll., vol. 117, no. 18, 82 p., 6 fig., 11 pl.

——, 1956, Paleocene mammalian faunas of the Bison basin in south-central Wyoming: Smithsonian Misc. Coll., vol. 131, no. 6, 57 p., 2 fig., 16 pl.

JEPSEN, G. L., 1930, Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming: Am. Philos. Soc., Proc., vol. 69, no. 7, p. 463–528, 3 fig., 10 pl.

——, 1940, Paleocene faunas of the Polecat Bench formation, Park County, Wyoming, Part 1: Am. Philos. Soc., Proc., vol. 83, p. 217–340, 22 fig. 5 pl.

MATTHEW, W. D., 1937, Paleocene faunas of the San Juan basin, New Mexico: Am. Philos. Soc., Trans., vol. 30, 510 p., 85 fig., 65 pl.

SIMPSON, G. G., 1935a, The Tiffany fauna, upper Paleocene, II.—Structure and relationships of *Plesiadapis:* Am. Mus. Novitates, no. 816, 30 p., 11 fig.

——, 1935b, The Tiffany fauna, upper Paleocene, III.—Primates, Carnivora, Condylarthra, and Amblypoda: Am. Mus. Novitates, no. 817, 28 p., 14 fig.

——, 1937a, The Fort Union of the Crazy Mountain field, Montana, and its mammalian faunas: U. S. Nat. Mus., Bull. 169, 287 p., 80 fig., 10 pl.

——, 1937b, Notes on the Clark Fork, upper Paleocene fauna: Am. Mus. Novitates, no. 954, 24 p., 6 fig.

VEATCH, A. C., 1907, Geography and geology of a portion of southwestern Wyoming: U. S. Geol. Survey Prof. Paper, no. 56, 178 p., 9 fig., 26 pl.

MANUSCRIPT RECEIVED DECEMBER 27, 1955.

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 712–713, MAY 1956

PALEONTOLOGICAL NOTE

AGASOMA SINUATUM FROM THE MIOCENE OF CUYAMA VALLEY, CALIFORNIA[1]

W. P. WOODRING
U. S. Geological Survey, Washington, D. C.

ABSTRACT—The muricid(?) gastropod *Agasoma sinuatum* (Gabb) occurs in the early upper Miocene Briones sandstone of the San Francisco Bay district. It also is found in Cuyama Valley, 200 miles south of San Francisco Bay, in strata correlated by Eaton with the late upper Miocene Neroly formation of the San Francisco Bay district.

Agasoma sinuatum (Gabb), a gastropod of peculiar and unmistakable outline, is the type and only species of the genus *Agasoma* (Gabb, 1869, p. 46; type designated by Cossmann, 1901, p. 147). Descriptions and illustrations of the species may be found in publications by Gabb (1866, p. 5; 1869, pl. 1, fig. 7), English (1914, p. 250, pl. 25, fig. 5,6) and Trask (1922, p. 158, pl. 8, fig. 2–4). It occurs in the Briones sandstone in the Coast Ranges east of San Francisco Bay. The Briones is the lowest of three formations in the San Pablo group of late Miocene age: Briones sandstone, Cierbo sandstone, and Neroly formation in ascending order. So far it has not been found in the other two formations of the San Pablo group in the San Francisco Bay district. Its lineage, however, is unknown. It appears abruptly without known predecessors and disappears as abruptly without leaving any known descendants. Under such circumstances it would be rash to conclude that the life span of the species coincides with the time span of the Briones sandstone, however empirically restricted its stratigraphic distribution may be in the San Francisco Bay district.

Though *Agasoma sinuatum* is generally thought of as a fossil of the San Francisco Bay district, it was found in 1914 by English in sandstone of late Miocene age in the hills on the south side of Cuyama Valley, in northern Santa Barbara County 200 miles south of San Francisco Bay, and was listed by him (English, 1916, p. 204). The specimen English collected is shown in Text-fig. 1, 2 (U. S. Geol. Survey locality 13021, saddle one mile west of Gene Johnson's house, near center of projected N.W. ¼, sec. 1, T. 9 N., R. 27 W., prominent *Pecten*-bearing bed in white sandstone about 50 feet below shale). English's specimen and record were not noticed until a few years ago, after the appearance of a publication by Eaton, Grant, & Allen (1941), which includes an account of the geology and paleontology of the upper Miocene deposits on the south side of Cuyama Valley. Echinoids of the genus *Astrodapsis* are extraordinarily abundant in these upper Miocene deposits and Eaton recognized numerous zones based on the distribution of lineages that include almost all the species in the San Pablo group of the San Francisco Bay district.

In 1949 the astrodapses collected by English at the locality that yielded *Agasoma sinuatum* were sent, without any locality data, to Eaton for identification. He identified two forms: a manuscript subspecies of *Astrodapsis cuyamanus* Kew (Eaton, Grant, & Allen, 1941, explanation of pl. 7, fig. 5, mentioned as an undescribed variety) and *A. blakei* Grant & Eaton (Eaton, Grant, & Allen, 1941, pl. 7, fig. 7). He also reported that the collection is characteristic of his zone 10 in his lower Neroly on the south side of Cuyama Valley (Eaton, Grant, & Allen, 1941, fig. 12); that is, in strata he correlated with the lower part of the Neroly formation of the San Francisco Bay district. When, later in the same year, English's specimen of *Agasoma sinuatum* was shown to Eaton, he remembered that he had found the species in his zone 10. One of Eaton's specimens, available through the kindness of U. S. Grant, is shown in Text-fig. 3–5. The locality is practically the same as English's (Univ. Calif., Los Angeles, locality

[1] Publication authorized by the Director, U. S. Geological Survey.

TEXT-FIG. *1–5*—*Agasoma sinuatum* (Gabb), ×1.
1,2—U. S. Geol. Survey locality 13021, USNM 562011.
3–5—Univ. California, Los Angeles, locality 1718, catalog 27800.

1718, Branch Canyon, zone 10, 25–50 feet below shale, on northeast flank of anticline, prominent *Pecten* reef striking across saddle). Under Eaton's guidance several incomplete specimens of *Agasoma sinuatum* were found at and near English's locality and also about 1½ miles to the northwest, also in Eaton's zone 10. The identification and zonal assignment of English's astrodapses inspire confidence in Eaton's lineages and his correlation of the upper Miocene deposits of Cuyama Valley with those of the San Pablo group of the San Francisco Bay district.

The Cuyama Valley occurrence throws no light on the lineage of *Agasoma sinuatum*. Though it adds to what is known about the stratigraphic and geographic distribution of the species, it adds one unrealistically restricted stratigraphic range to another. Such occurrences, unsupported by real knowledge concerning the evolution of a species, are not unusual and, in the absence of evidence to the contrary, are likely to be seized upon for exact correlation.

The spine on the outer lip, alined with a narrow indentation on the body whorl, and the unexcavated columellar lip suggest that *Agasoma* is allied to *Forreria* and is to be assigned to the Muricidae, despite the absence of axial lamellae. The spine, which is shown in Text-fig. 3, 4, was noticed by Trask (1922, p. 157–158), but was interpreted to indicate thaidid affinities.

REFERENCES

COSSMANN, M., 1901, Essais de paléoconchologie comparée, pt. 4, 293 p., 10 pl.

EATON, J. E., GRANT, U. S., & ALLEN, H. B., 1941, Miocene of Caliente Range and environs, California: Am. Assoc. Petroleum Geologists Bull., vol. 25, p. 193–262, 9 pl., 14 fig.

ENGLISH, W. A., 1914, The *Agasoma*-like gastropods of the California Tertiary: California Univ., Dept. Geol. Bull., vol. 8, no. 10 p. 243–256, pl. 24, 25.

——, 1916, Geology and oil prospects of Cuyama Valley, California: U. S. Geol. Survey Bull. 621, p. 191–215, pl. 19–21, fig. 12.

GABB, W. M., 1866, 1869, Cretaceous and Tertiary fossils: California Geol. Survey, Paleontology, vol. 2, p. 1–38, 1866; p. 39–299, 36 pl., 1869.

TRASK, P. D., 1922, The Briones formation of middle California: California Univ., Dept. Geol. Sci. Bull., vol. 13, no. 5, p. 133–174, pl. 1–8.

MANUSCRIPT RECEIVED JANUARY 26, 1956.

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 714–730, PL. 75–77, 6 TEXT-FIG., MAY 1956

TETHYAN JURASSIC HYDROIDS OF THE FAMILY MILLEPORIDIIDAE

R. G. S. HUDSON
Iraq Petroleum Company Limited, London, England

ABSTRACT—The lectotype of *Milleporidium remeši* Steinmann, 1903a, the type species of its genus, and that of *Stromatopora romanica* Dehorne, 1918, are redescribed and the latter species made the type of *Steineria* Hudson, n. gen., to which genus *Milleporidium somaliense* Zuffardi-Comerci, 1931, is now allocated. The allocation by Zuffardi-Comerci (1931) of *Stromatopora lusitanica* Dehorne, 1920, to *Milleporidium* is confirmed. As the holotype of *Promillepora pervinquieri* Dehorne, 1920, the type species of its genus, is lost, the species is redescribed and figured from specimens from the Kurnub Limestone (Upper Jurassic) of Southern Israel. From this locality *Promillepora kurnubi* Hudson, n. sp., is also described. *Stromatopora douvillei* Dehorne, 1918, is allocated to this genus.

In these genera and in *Myrioporina* Kühn, 1939, *Shuqraia* Hudson, 1954b, and *Sporadoporidium* Germošvek, 1954, the coenosteum is traversed by autotubes. These, the zooidal tubes or zooecia of other authors, are regular, vertical, tabulate tubes, individually often dimorphic, sharply differentiated from the coenosteal-tubules. They may be associated with lateral tubes, which are periodically developed, not so sharply differentiated, generally radially arranged, and may link the autotubes. Such autotubes are considered to be the distinctive structures of the Milleporidiidae, linking that family with the Hydroidea.

Shuqraia, *Promillepora*, and *Steineria* are a morphological series proceeding from non-latilamellate forms with autotubes hardly distinguishable from the coenosteal-tubules to complex latilamellate forms in which the autotubes are periodically wide and narrow.

INTRODUCTION

THE numerous Jurassic hydroids, stromatoporoids and spongiomorphs collected by the geologists of the Iraq Petroleum Company Limited from the Middle East include species comparable to those founded by Dehorne (1920) on specimens from the Jurassic rocks of the countries bordering the Mediterranean, rocks formed, as were those in the Middle East, in the Tethyan province of sedimentation. Certain of Dehorne's species placed by her in the genus *Stromatopora* were in 1927 and 1928 allocated by Kühn to *Milleporidium* Steinmann, a genus considered by Kühn to belong to the Hydroidea: later they were returned by Lecompte (1952) to the Stromatoporoidea. The issue depends mainly on the interpretation of the function of the sharply differentiated wider tubes which occur in the coenosteum of such species: Lecompte considers that they are part of the astrorhizal system; Kühn that they are zooidal tubes comparable to those characteristic of the Milleporidae. Such species include *Stromatopora romanica* Dehorne, 1918, *S. arrabidensis* Dehorne, 1920, and *S. douvillei* Dehorne, 1918, respectively based on single specimens from the Upper Jurassic of Roumania, Portugal and Tunisia. By the courtesy of Professor P. Pruvost it has been possible to borrow from the collections of the Geological Laboratory of the Sorbonne the lectotypes of these species and, for comparison, a syntype of *Milleporidium remeši* and so reinvestigate their structure, discuss their systematic positions, and facilitate the identification of certain of the Middle East forms.

In her 1920 paper Dehorne also founded the genus *Promillepora* with the type species *Promillepora pervinquieri* Dehorne. This species she considered was a hydroid closely related to *Millepora* Linné: it is also structurally comparable to *Milleporidium*. The species, and related forms, are common in the Middle East, and since its internal structure has never been described and since its lectotype is lost, Middle East specimens are here described and figured.

This work has been carried out, by the kind permission of Mr. F. E. Wellings, Chief Geologist, Iraq Petroleum Company Limited, at the Geological Research Centre

of that Company as part of a project entailing the description of the Mesozoic stromatoporoid faunas of the Middle East.

MILLEPORIDIOID SKELETAL STRUCTURES

Coenosteum.—The greater part of the milleporidioid skeleton consists of the coenosteum (coenenchyme, coenosarceal tissue *auctt.*), the skeletal tissue formed of transverse and vertical coenosteal-lamellae, and tabulae. The pattern of the network (the coenosteal-reticulum) formed by the lamellae depends on the relative part played by the vertical and transverse elements in its formation and their relative thickness, continuity and regularity. It may be entirely tubular, as in *Milleporidium*, formed by vertical coenosteal-tubules which, in cross section, may be elongate and tortuous (vermiculate), or irregularly circular: it may consist of a fairly regular lattice, as in part of the coenosteum of *Steineria*, in which transverse lamellae are equally as important as the vertical lamellae: or it may consist of an irregular mesh, as in *Promillepora*, in which vertical and transverse lamellae are not always individually distinct.

Latilamellae.—The peripheral coenosteum of the Milleporidiidae is often formed of concentric layers alternately differing the one from the other in the relative dominance of vertical and transverse lamellae. Such are latilamellae—they should be clearly distinguished from pseudolatilamellae, concentric layers of the coenosteum due to cessation and renewal of growth. The two types of reticula characteristic of these latilamellae are here referred to, for want of better terms, as coarse-textured and fine-textured. In the former the reticulum mainly consists of vertical coenosteal-tubules, variously vermiculate in cross section, the vertical lamellae forming them being usually thicker than in the fine-textured latilamellae. In the latter, transverse lamellae are important or even dominant so that, in vertical section, the reticulum is a regular or lamellate lattice and, in transverse section, a mesh of tubule openings which are less elongate and more generally circular than those in the coarse-textured latilamellae.

Autotubes.—In his original description of *Milleporidium*, Steinmann (1903a) drew attention to the occurrence in the skeletal tissue of straight, tabulate tubes markedly wider than the coenosteal-tubules. These he compared with the zooidal tubes of *Millepora* denying their equivalence to the tortuous and branching "zooid tubes" described by Nicholson as occurring in the Stromatoporoidea. In recent years the term "zooidal tubes" has been used in descriptions of Stromatoporoidea and Hydroidea with many connotations; Steiner (1932) for instance, considers all tabulate tubes to be "zooidal tubes." To avoid this confusion and to avoid any implication of function, these structures of the Milleporidiidae are referred to in this paper as autotubes (zooidal tubes, major tubules *auctt.*).

In *Milleporidium*, *Steineria*, and *Promillepora* there are also tabulate tubes of about the same width as the coenosteal-tubules but differing from them in that they are more regular since they are straighter, more continuous, more definitely walled, and more definitely circular in cross section (they are better recognized on polished surfaces than in thin section). These narrow tabulate tubes pass into the wider autotubes which in turn revert to the narrow tubes, a change in width which may take place periodically. Since the narrow and wide tabulate tubes are structurally similar they are both termed autotubes. These narrow autotubes also occur in *Shuqraia* and *Myrioporina*, neither of which has wide autotubes.

Lateral tubes.—Within the reticulum there are also, at various levels, lateral channels (lateral tubes within the reticulum, lateral canals on the surface) open both to the autotubes and the coenosteal-tubules. Though they are very differently developed in the various genera, they are, in general, parallel to the transverse lamellae and are bounded by the vertical lamellae, differing from the interspaces between these only by their greater continuity and their tendency to radial grouping. Like the interspaces they are generally vermiculate, not of constant width, and not walled. When associated with the wide autotubes they are wider than the coenosteal-tubules but not as wide as the autotubes. In the fine-textured latilamellae they are no wider than the coenosteal-tubules and are only distinguished by their radial grouping round the narrow autotubes.

Ostea.—The apertures on the surface of both the coenosteal-tubules and the autotubes.

MORPHOLOGICAL GROUPING

It seems likely that genera, such as *Myrioporina* and *Shuqraia*, with narrow autotubes only, were morphologically ancestral to those with both narrow and wide autotubes such as *Promillepora*, *Steineria*, and *Milleporidium*. *Shuqraia* and *Promillepora*, for instance, have a comparable reticulum pattern and are probably closely related. The reticulum patterns of *Myrioporina* and *Milleporidium* are also closely similar and these genera are also probably members of a morphological series. It is also probable that genera such as *Promillepora* with long wide autotubes and little latilamellation are morphologically ancestral to those such as *Steineria* with marked latilamellation and short and concentrically arranged wide autotubes. *Shuqraia*, *Promillepora*, and *Steineria* are thus a morphological series proceeding from a non-latilamellate form with autotubes hardly distinguishable from the coenosteal-tubules to complex latilamellate forms in which the autotubes are periodically wide and narrow. It is doubtful if the genera discussed in this paper are phylogenetic units: they are probably composite morphological genera, the key to phylogenetic relationship being probably the pattern of the coenosteal reticulum.

SYSTEMATIC PALEONTOLOGY

Order HYDROIDEA Dana, 1846

Family MILLEPORIDIIDAE Yabe & Sugiyama, 1935

Diagnosis.—Hydroidea with vertical and transverse lamellae forming a coenosteal-reticulum, generally vertically tubular, variously tabulate, and traversed by regular, tabulate, vertical autotubes. Lateral tubes absent or variously developed. No mamelons or astrorhizae. Skeletal tissue of lamella fibrous, fasciculate outwards and upwards from a medial plane or axis.

Remarks.—The concept of the Milleporidiidae has thus been enlarged to include not only those genera, as *Milleporidium*, *Steineria*, *Promillepora*, with both wide and narrow autotubes but also such genera as *Shuqraia* and *Myriopoṛina* with narrow autotubes only.

The Milleporidiidae are considered to be transitional between the Stromatoporoidea and the Hydroidea and, as such, they have been variously allocated to the former order (Dehorne, 1920; Steiner, 1932; Zuffardi-Comerci, 1931; Yabe & Sugiyama, 1935; Lecompte, 1952) or the latter (Steinmann, 1903; Kühn 1928, 1939; Alloiteau *in* Piveteau, 1952; Germovšek, 1954). The author is of the opinion that morphologically they are more closely comparable to the Hydroidea than to the Stromatoporoidea and therefore are better allocated to the former order.

Genus MILLEPORIDIUM Steinmann, 1903

Milleporidium STEINMANN, 1903a, p. 1; 1903b, p. 131; 1907, p. 150; KÜHN, 1927, p. 550; 1928, p. 86; 1939, p. 34; ZUFFARDI-COMERCI, 1930, p. 27; STEINER, 1932, p. 82; YABE & SUGIYAMA, 1935, p. 100; LECOMPTE, 1952, p. 31; ALLOITEAU, 1952, p. 382.

Type species (by monotypy).—*Milleproidium remeši* Steinmann, 1903a.

Diagnosis.—Milleporidiidae with vertical lamellae regular and continuous, transverse lamellae generally subordinate and, like the tabulae, often aligned, the lamellae together forming a regular, latilamellate coenosteal-reticulum. Autotubes periodically short and wide or narrow and long, forming alternate dimorphic and monomorphic reticula. Lateral tubes very subordinate.

MILLEPORIDIUM REMEŠI Steinmann, 1903

Pl. 75, figs. 5–8; Text-fig. 1

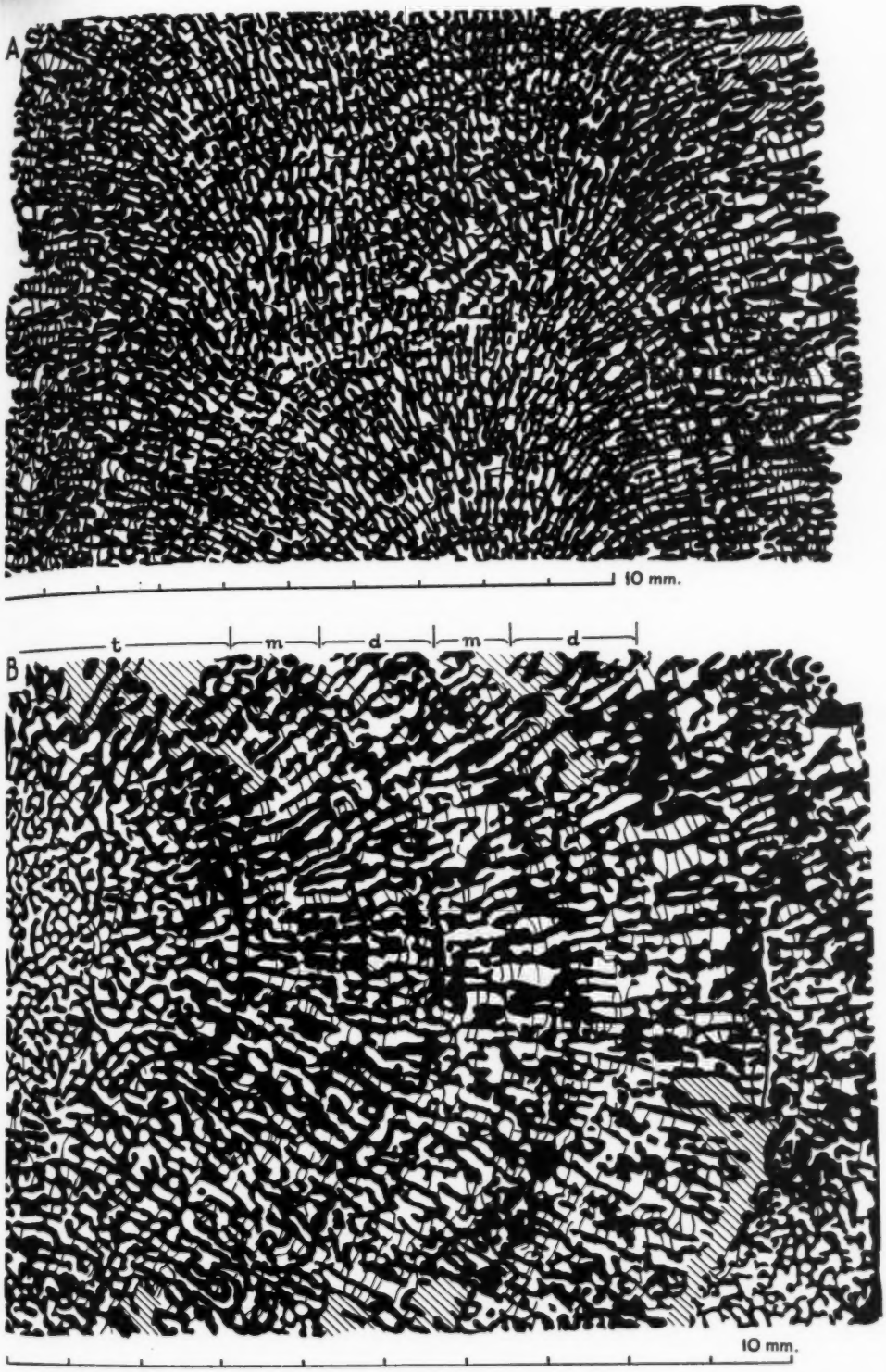
Milleporidium Remeši STEINMANN, 1903a, p. 1–8, pl. 2, figs. 1–6, STEINMANN, 1903b, p. 131, text-fig. 184BC; REMEŠ, 1905, p. 33; STEINMANN, 1907, p. 150, text-fig. 216; KÜHN, 1927, p. 550; 1928, p. 87; 1939, text-fig. 47; STEINER, 1932, p. 83, 107.

Stromatopora Remesi, DEHORNE, 1920, p. 82.

Milleporidium remesi, YABE & SUGIYAMA, 1935, p. 186; LECOMPTE, 1952, p. 32.

not *Milleporidium remesi?* YABE & TOYAMA, 1927, p. 117–119, pl. 12, fig. 1,2.

Syntypes.—The five specimens described and figured by Steinmann, 1903a, pl. 1, fig. 1–8, pl. 2, fig. 1–6, are stated to be from the Tithonian of Stramberg, Moravia, Czechoslovakia. These specimens were collected by M. Remeš from Ryachalitz (Mähren), Czecho-Slovakia, from exotic blocks of Stramberg limestone (Remeš, 1905) and, with the exception of that here made the holotype, are now in the collec-



TEXT-FIG. *1*—*Milleporidium remeši* Steinmann, Outline diagrams of thin sections of lectotype, specimen 31 (see text). Line hachuring represents mud layers. *A*, part of slightly oblique longitudinal axial section 31c. *B*, part of transverse section 31b, showing axial, (t) transitional, (m) fine-textured, and (d) coarse-textured dimorphic peripheral reticula. Section adjacent to that of Pl. 75, fig. 9.

tions of the Geological—Palaeontological Department, Natural History Museum, Vienna. Their nomination by Lecompte (1952, pl. 31) as the holotype is invalid.

Lectotype.—The syntype now in the Stromatoporoid collection, Geological Laboratory, Sorbonne, Paris, numbered 31, with thin sections 31a-c cut from it, and figured in this paper Pl. 75, fig. 5–8, and Text-fig. 1.

Diagnosis.—*Milleporidium* of phaceloid columns with a common base. Reticulum axial and peripheral, the latter markedly latilamellate. Fine-textured latilamellae consist of transverse lamellae and tabulae, well developed and markedly aligned, and vertical lamellae forming coenosteal-tubules, walls and tubules each about 0.05 mm. across. In coarse-textured latilamellae, vertical lamellae are about 0.06 mm. thick and tubules up to 0.1 mm. across. Narrow and wide autotubes respectively about 0.1 mm. and 0.3 mm. across, the latter, mainly in the coarse-textured latilamellae, forming a marked dimorphic reticulum. Lateral tubes slightly developed.

*Description.**—Coenosteum of slightly tapering, stumpy, phaceloid columns (Stnm. pl. 1, fig. 1). Surface, finely papillose, patterned by a fine, approximately circular mesh in which there may be groups of autotube ostea. Reticulum axial and peripheral, the latter being markedly latilamellate (Pl. 75, fig. 5). Axial reticulum of vertical tubes, irregularly polygonal or loosely vermiculate, slightly tabulate and of varying diameter, commonly 0.08 mm. to 0.13 mm. Tubule walls (about 0.04 mm. to 0.06 mm. thick), slightly irregular but generally parallel, consist of pillars and joining pillar-lamellae (Stnm., pl. 2, fig. 3). The latilamellae of the peripheral reticulum are alternately fine and coarse-textured (Text-fig. 1B and Pl. 75, fig. 5).

In the fine-textured reticulum vertical and transverse elements are equally developed forming a marked rectangular lattice in longitudinal sections (Pl. 75, fig. 5). The transverse elements may be lamellae formed by a thickening of the pillars at individual levels (Text-fig. 1A and Stnm., pl. 1, fig. 4,8), or aligned and sometimes thickened tabulae (Stnm., pl. 2, fig. 3 and fig. 5 where l′ are transverse lamellae and l″ are aligned tabulae). The vertical lamellae, about 0.045 mm. thick, form the coenosteal-tubules, about 0.055 mm. across and either circular, or slightly elongate and vermiculate: occasionally a vague stellate

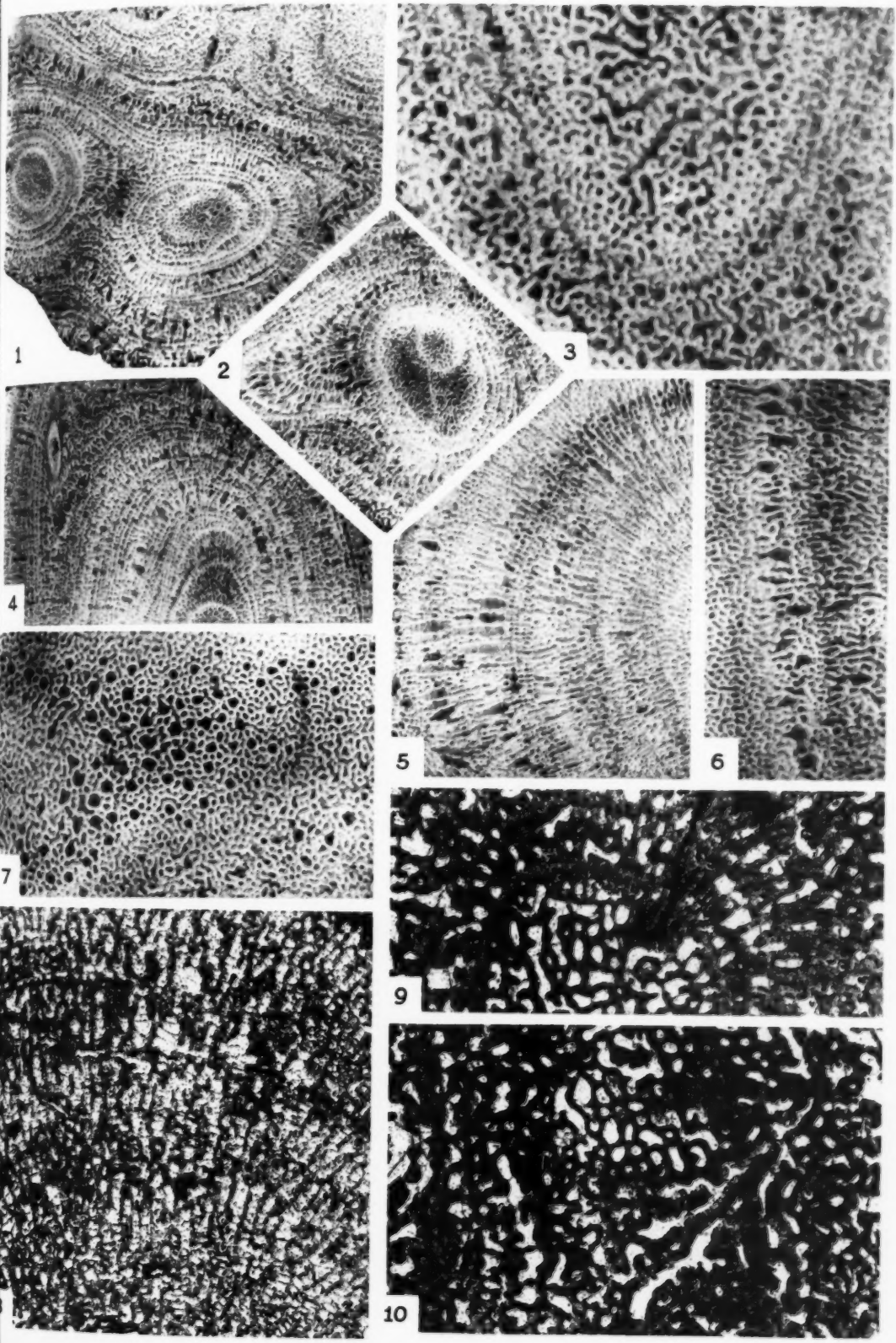
* In this description the reference Steinmann, 1903a, is shortened to Stnm.

Explanation of Plate 75

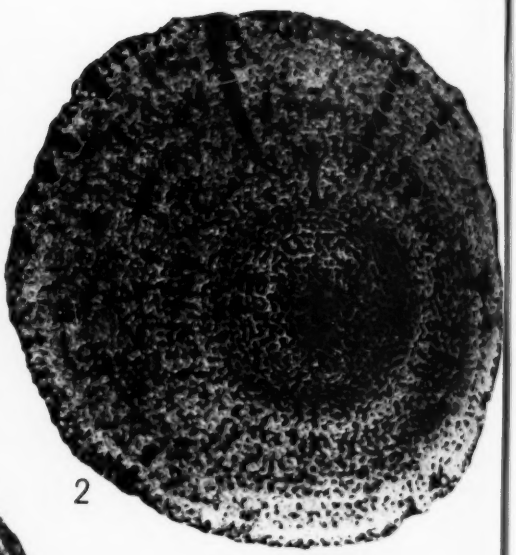
Fig. *1–4*—*Steineria romanica* (Dehorne). Polished surfaces, photographed by reflected light, of lectotype, specimen 27, Stromatoporoid collection, Geological Laboratory, Sorbonne, Paris; Jurassic, Dobrogea, Roumania. *1*, transverse surface, ×3.3, of column C, showing coarse and fine-textured latilamellae, the former with wide autotubes; *2*, transverse surface, ×3.3, of column A, showing beginning of division into new columns; *3*, tangential surface, ×8.2, of column B (from upper right of fig. 4) showing wide autotubes and lateral tubes of coarse-textured reticulum, and narrow autotubes of fine-textured reticulum; *4*, oblique longitudinal surface, in part axial, ×3.3, of column B showing continuation of narrow autotubes into wide autotubes. (p. 723)

5–8—*Milleporidium remeši* Steinmann. *5–7*, polished surfaces and, *8*, thin section of lectotype, specimen 31, Stromatoporoid collection, Geological Laboratory, Sorbonne, Paris; Tithonian, Stramberg, Moravia, Cezchoslovakia. *5*, transverse surface, ×5.75, showing fine and coarse-textured latilamellae with wide and narrow autotubes; *6*, longitudinal axial surface, ×7.4, showing coarse and fine-textured latilamellae and autotubes: surface of column to right; *7*, tangential surface, ×7.4, showing variation in width of autotubes; *8*, part of transverse section, ×11, showing tabulae. (p. 716)

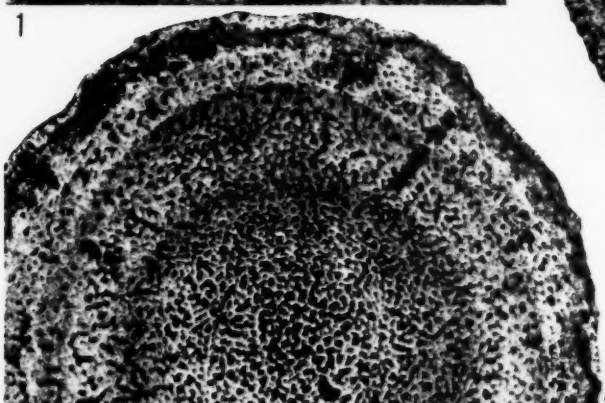
9,10—*Steineria romanica* (Dehorne). Longitudinal thin sections, 27c and 27e, photographed in transmitted light, ×11, of column B of lectotype specimen 27. *9*, lower middle part is a transverse section of extension from coarse-textured reticulum, initiating division into new columns (see Pl. 75, fig. 2); *10*, middle part is tangential of coarse-textured reticulum showing lateral tubes. (p. 723)


1
2
3
4
5
6
7
9
10

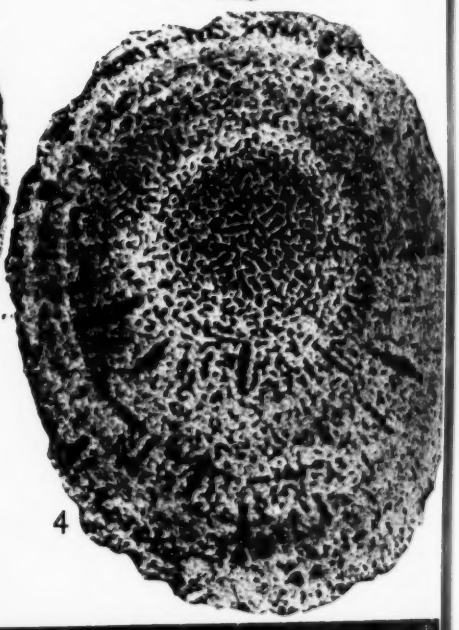
1



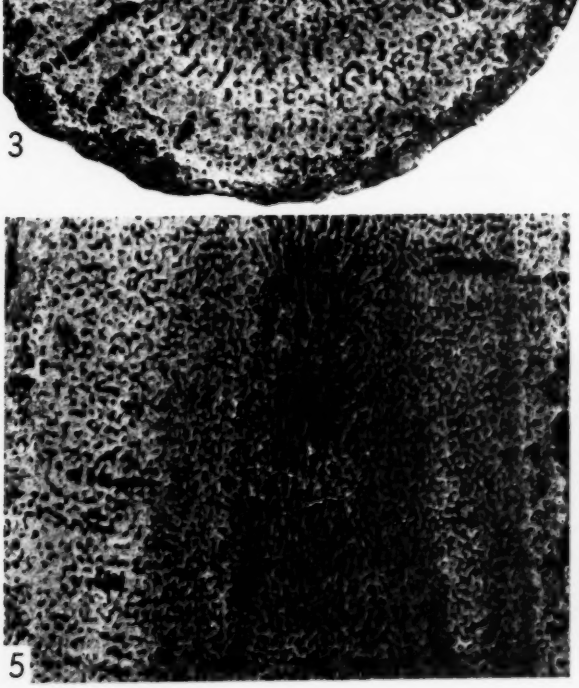
2



3



4



5

6

arrangement or grouping around autopores (Stnm., pl. 1, fig. 3) as in Myrioporina.

In the coarse-textured reticula, the dominant vertical lamellae, about 0.05 mm. to 0.07 mm. thick, form coenosteal tubules (about 0.04 mm. to 0.1 mm. across) with a coarse vermiculate mesh.

Autotubes occur throughout the peripheral reticulum in both the fine and coarse-textured latilamellae. They commence in the axial reticulum as straight, walled, narrow, tabulate tubes not crossed by transverse lamellae or thickened tabulae (Pl. 75, fig. 6,7, and Stnm., pl. 2, fig. 2). In the peripheral reticulum they are both wide (generally 0.3 mm. across) and narrow (generally 0.1 mm. across), the wide growth-phase occurring mainly though not exclusively in the coarse reticulum: they thus form alternate dimorphic and monomorphic reticula (Stnm., pl. 1, fig. 7; pl. 2, fig. 4b,c-b is monomorphic and c dimorphic). Though the wide autotubes vary in width, being about 0.2 mm. in the fine-textured reticulum (Pl. 75, fig. 7) and about 0.3 mm. in the coarse-textured reticulum, they are always distinct from the narrow autotubes and the coenosteal tubules. The transition between wide and narrow autotubes is usually abrupt (Pl. 75, fig. 5,6,8). The wide autotubes are often linked by a break in their wall to a neighbouring coenosteal tubule (Stnm., pl. 1, fig. 6) or to what may be small lateral tubes (Pl. 75, fig. 6, and Stnm., pl. 1, fig. 5). Steinmann (Stnm., p. 4) considers that these lateral tubes occur especially in the layers where the wide autotubes are beginning to form (Pl. 75, fig. 7).

The microstructure of the skeletal elements is not well preserved. It is microfibrous outwards and, apparently, slightly upwards, from an axis, or medial plane.

MILLEPORIDIUM LUSITANICUM (Dehorne), 1920

Stromatopora milleporoides var. *lusitanica* DEHORNE, 1920, p. 88, pl. 8, fig. 5,13, pl. 16, fig. 8.
Stromatopora milleporoides, *S. milleporoides* de *lusitanica*, and *S. milleporoides* var. *lusitanica*, DEHORNE, 1923, p. 18. pl. 2, fig. 3a,3b.
Milleporidium lusitanicum, ZUFFARDI-COMERCI, 1931, p. 71.
Milleporidium milleporoides var. *lusitanica*, KÜHN, 1927, p. 551; 1928, p. 87.
Milleporidium milleporoides, YABE & SUGIYAMA, 1935, p. 160; WELLS, 1943, p. 82.
Milleporidium cf. *lusitanicum* HUDSON, 1955a, p. 238.

Synonymy.—For validity of the species name '*lusitanicum*' see discussion on the synonymy of *Steineria romanica* (Dehorne).

Lectotype.—Thin transverse section figured, as *Stromatopora milleporoides* var. *lusitanica* Dehorne, in Dehorne, 1920, pl. 8, fig. 5, and pl. 16, fig. 8, and in Dehorne, 1923, pl. 2, fig. 3b. From Lusitanian of the tunnel of Chão de Maçãs, Portugal.

Diagnosis.—*Milleporidium* of phaceloid columns (lectotype: largest diameter 25 mm., smallest about 7 mm.). Reticulum axial and peripheral, the latter narrowly latilamellate. Vertical lamellae, markedly dominant, about 0.05 mm. to 0.07 mm. thick, fairly straight and continuous; coenosteal-tubules about 0.05 mm. to 0.1 mm. across. Transverse lamellae often aligned. Wide autotubes (about 0.2 mm. to 0.3 mm. across), short, not abundant, mainly in outer part of peripheral reticulum; narrow

---

EXPLANATION OF PLATE 76

Promillepora pervinquieri Dehorne, 1920. Thin sections, ×6.6, photographed by reflected light, of H 4905 (fig. 2,4) and H 4906 (fig. 1,3,5,6) from upper part of Kurnub Limestone (Upper Jurassic) of Makhtesh Hathira, southeast of Beersheba, northern Negev, Israel. (p. 720)

FIG. *1,5,6*—Serial longitudinal sections of H 4906. *1*, 4906f, tangential section (base of section to left) of compact reticulum. Note tendency to radially patterned reticulum around narrow autotubes; *5*, 4906d, axial, showing wide transitional reticulum with well-developed transverse lamellae; *6*, 4906e, section between those of fig. 1 and 5 showing in centre tangential section of transitional reticulum.

2,4—Serial transverse sections of H 4905. *2*, 4905c, showing development of wider transitional zone; *4*, 4905, a earlier part of coenosteal column.

3—Transverse section H 4906b showing wide transitional reticulum.

autotubes (up to 0.15 mm. across) longer and abundant; periodical development not marked, mainly in outer part of peripheral reticulum.

Remarks.—The pattern and scale of the coenosteal-reticulum, particularly the dominance of the vertical lamellae, and the occurrence of long narrow autotubes, link *M. lusitanicum* with *Milleporidium remeši* and *Myroporina*. Morphologically it is intermediate between these two forms, possessing wide autotubes which do not occur in *Myrioporina* and lacking the marked periodicity and clear cut dimorphism of *Milleporidium remeši*.

Genus PROMILLEPORA Dehorne, 1920

Promillepora, KÜHN, 1939, p. 34.

Type species (by monotypy).—*Promillepora pervinquierei* Dehorne, 1920.

Diagnosis.—Milleporidiidae with irregular, discontinuous, and approximately equally developed vertical and transverse lamellae, forming an irregular coenosteal-mesh. Narrow and wide autotubes, the latter of variable length, often extending through greater part of peripheral reticulum. Lateral tubes irregular and slightly developed.

Remarks.—*Promillepora* is similar to *Milleporidium* and was considered to be a synonym (Kühn, 1939, p. 34). The main differences are that in *Promillepora* the transverse lamellae play a greater part in the formation of the coenosteal-reticulum, both transverse and vertical lamellae and the consequent reticulum are much more irregular, the narrow and wide autotubes are fewer, of very variable length, not periodically developed and there is less evidence of transition between them. These differences justify the retention of the genus.

The reticulum of *Promillepora* is very similar to that of *Shuqraia* Hudson, 1954b, which, however, has narrow but no wide autotubes.

PROMILLEPORA PERVINQUIERI Dehorne, 1920

Pl. 76, fig. 1–6

Lectotype (here chosen).—Specimen figured by Dehorne (1920, fig. 12, pl. 8) and sections cut from it. From *Stromatopora douvillei* beds, Upper Jurassic (?Sequanian), near Tatahouine, southernmost Tunisia (see Hudson, 1955b, for locality references). Formerly in Pervinquière collection, Geological Laboratory, Sorbonne, Paris: now lost.

Remarks.—The type specimen of this species is lost and no topotypes which can be definitely allocated to the species are available. Dehorne's description (1920, p. 97, 98, 100) is, however, adequate for specific recognition and the diagnosis and description given below are based on that description, supplemented by the examination of specimens from the Middle East from beds of the same age and belonging to the Tethyan province of sedimentation.

Diagnosis.—*Promillepora* of branching columnar coenostea up to 15 mm. diam. Surface finely meshed with dimorphic ostea. Axial and peripheral reticula of both vertical and transverse lamellae irregularly developed; in the transitional reticulum the latter may be dominant and often aligned. Peripheral reticulum slightly latilamellate. Narrow autotubes, about 0.12 mm. wide, commencing in axial reticulum and sporadically developed across the peripheral reticulum. Wide autotubes, about 0.25 mm to 0.30 mm. across, not abundant, some extending across peripheral reticulum.

Middle East material.—Specimens H 4905* (2 pieces) and thin sections a-c (Pl. 76, fig. 2,4); H 4906 (2 pieces) and thin sections a-f (Pl. 76, fig. 1,3,5,6); H 4899 (4 pieces) and thin section a ("*Stromatopora*" grown on and completely surrounding *Promillepora*); H 4904 (1 piece) and thin section a (branchs at about 40° to main column). Collected by L. Damesin from upper part of Kurnub limestone, Makhtesh Hathira (northwest flank through crest maxima), southeast of Beersheba, northern Negev, Israel. For details of section see Ball & Ball (1953) and Wiener (1955).

Description.—Coenosteum of cylindrical columns, generally 12 mm. to 15 mm. across, occasionally branching (Dehorne, 1920, pl.

* In this paper numbers preceded by H are the registration numbers of the specimens in the collections of the Dept. of Geology, British Museum (Natural History), London.

8, fig. 12). Initial coenosteum not known. Surface a fine irregular network of lamellae with rounded or irregularly elongate mesh and, occasionally, ostea of autotubes. Coenosteal-reticulum of vertical and transverse lamellae with pillars and joining lamellae still evident. Axial reticulum, about 0.25 to 0.30 of diameter of column, of irregular and often discontinuous vertical lamellae, about 0.03 mm. to 0.04 mm. thick, forming in transverse section a wide and often continuous mesh, generally 0.10 mm. to 0.20 mm. across, with thin walls sharply flexed at pillars. Tabulae and transverse lamellae rare. Peripheral reticulum of very irregular vertical and transverse lamellae, often not distinguishable and forming an irregular net in which the lamellae are as wide as or wider than the interspaces. Interspaces, about 0.10 mm. across, transversely round, or elongate and tortuous but short, often connected by narrow canals. Reticulum tends towards concentric latilamellae of fine and coarse-textured reticula in which the lamellae are respectively 0.10 mm. to 0.15 mm. and 0.15 to 0.20 mm. thick, the lamellae in the former tending to be discontinuous, the interpsaces in the latter being narrower. Between the axial and peripheral reticulum there is a transitional reticulum characterized, as in other genera, by a dominance of transverse lamellae, discontinuous though often aligned. As the vertical lamellae are discontinuous and not well developed, the reticulum is here gengerally concentrically lamellate.

The autotubes are of two distinct widths, either about 0.25 mm. to 0.30 mm. or about 0.12 mm.; transitional widths are very rare. Both wide and narrow autotubes are evenly tabulate. The wider autotubes may cross the entire peripheral reticulum commencing at its junction with the transitional reticulum and continuing to the surface of the coenosteum, or they may be short, arising from and continued by narrow autotubes. They tend to be equally spaced in the reticulum, about 1.2 mm. apart at the surface, to develop on one side rather than the other, and to occur vertically the one above the other so that on the surface and in tangential section (Pl. 76, fig. 6) they are aligned. At intervals they commun cate either directly or by narrow canals to the coenosteal-tubules. The narrow autotubes are about 0.12 mm.; wide. In the peripheral reticulum they are generally straight, of constant width and continuously walled: in the transitional reticulum they are more irregular. They commence early in the transitional and possibly in the axial reticulum. They, also, are linked to the coenosteal-tubules.

Lateral tubes are short, irregular, and not common. They are about 0.12 mm. wide, and tend to be grouped around and to be continuous with both the wide and narrow autotubes.

The skeletal tissue of the lamellae is finely fibrous (best visible between crossed nicols); the fibres of the vertical lamellae are directed upwards and outwards from a medial plane or axis; those of the transverse lamellae are continuous with those of the vertical lamellae and are directed upwards.

PROMILLEPORA KURNUBI, n. sp.
Pl. 77, fig. 3–11; Text-fig. 6

Type specimens.—Holotype: H 4898 (1 piece) and thin section a (Pl. 77, fig. 5 and text-fig. 6). Paratypes: H 4896 (2 pieces) H 4900 (1 piece) and thin section a (Pl. 77, fig.4); H 4901 (2 pieces) and thin sections a-c (Pl. 77, fig.3); H 4902 (1 piece) (Pl. 77, fig. 6–11) and thin sections a-d. H 4900–2 are possibly parts of one individual. Collected by A. H. Smout from the Kurnub Limestone (Upper Jurassic), Maktesh Hathira, southeast of Beersheba, northern Negev, Israel.

Description.—Promillepora of branching coenosteal columns up to 40 mm. across (largest fragment 90 mm. long). Surface a fine net with an irregularly circular or slightly elongate mesh and evenly distributed wide and narrow autotube ostea, slightly rimmed. Axial coenosteal-tubules about 0.2 mm. across with walls about 0.06 mm. to 0.08 mm. thick. Coenosteal-tubules of peripheral reticulum about 0.1 mm. across with walls about 0.15 mm. thick. Often radially arranged around narrow autotubes. Peripheral reticulum with coarse, and fine-textured latilamellae. Vertical lamellae dominant in coarse-textured latilamellae; transverse lamellae dominant, and often aligned, in fine-textured latilamellae. Transition

zone with abundant aligned transverse lamellae. Wide autotubes, common, about 0.3 mm. across, variable in length, occur mainly in coarse-textured reticula but often cross both fine and coarse-textured reticula. Narrow autotubes long and start in axial zone. Lateral tubes narrow and not readily distinguishable.

Remarks.—Both latilamellae and the wide autotubes increase in number with the growth of the coenosteal branches, the latilamellae decreasing in width. The species is closely related to *P. pervinquieri* than which it is more structurally advanced.

PROMILLEPORA DOUVILLEI (Dehorne), 1918

Compare *Stromatopora douvillei* DEHORNE, 1918, 1920; ZUFFARDI-COMERCI, 1938; WELLS, 1943, HUDSON, 1955b.
Milleporidium Douvillêi, KÜHN, 1927, 1928.
Stromatopora douvillêi, STEINER, 1932.
Stromatoporina douvillêi, LECOMPTE, 1952; HUDSON, 1954a.
Shuqraia cf. *Stromatopora douvillêi*, HUDSON, 1954b.

Lectotype (chosen Lecompte, 1952, p. 23).—Thin transverse section figured, as *Stromatopora douvillêi* Dehorne, in Dehorne, 1920, pl. 9, fig. 9, and in Hudson, 1955b, text-fig. 1. From *Stromatopora douvillêi* beds, Upper Jurassic (?Sequanian) of Guelb-el-Anze, Southernmost Tunisia (see Hudson, 1955b, for locality references). Specimen 29/1, Stromatoporoid collection, Geological Laboratory, Sorbonne, Paris.

Middle East material.—Specimen H 4903 (1 piece) and thin section a-l. Collected by L. Damesin from upper part of Kurnub Limestone (Upper Jurassic) of Makhtesh Hathira, southeast of Beersheba, northern Negev, Israel. The specimen is phaceloid, with maximum branch diameter about 20 mm. It is slightly more latilamellate and is probably a more mature example of the species, the type of which is probably from a young branch.

Diagnosis.—*Promillepora* with columnar coenosteum (diam. of type: 12 mm.) with axial and peripheral reticula, the latter, tending to be concentrically patterned and slightly latilamellate, consists of irregular transverse and vertical lamellae, about 0.12 mm. thick, and small irregular interspaces. Wide autotubes, few, short, about 0.2 mm. to 0.3 mm. across, sporadically distributed, tending to be concentrically alighed. Narrow autotubes few and rarely definite. Lateral tubes irregular and not definite.

Generic allocation.—The type material of this species, other than the lectotype thin section, used by Dehorne (1918, 1920) for the foundation of her species has either been lost or allocated to other genera and species (Lecompte, 1952; Hudson, 1955b). Former specific interpretation and generic allocation have thus varied considerably. The description by Hudson (1955b) and the above diagnosis are based on the lectotype which shows that the species is certainly a member of the Milleporidiidae. The pattern of the coenosteal-reticulum is closely similar to that of *Promillepora pervinquieri* and though that species has both short and long wide autotubes and *P. douvillêi* only short ones there are undescribed forms which link the two species, forming a morphological group which can be accommodated without difficulty in the above diagnosis of *Promillepora*.

Genus STEINERIA, n. gen.

Romanactis MUNIER-CHALMAS nom. nud., MS. in coll. (see Dehorne, 1920, p. 88).

Type species (here chosen).—*Stromatopora romanica* Dehorne, 1918.

Diagnosis.—Milleporidiidae with a latilamellate tubular peripheral reticulum in which irregular vertical lamellae and regular and aligned transverse lamellae are alternately dominant forming alternate coarse and fine-textured reticula. Tabulae often aligned and continuous. Autotubes both narrow and long and wide and short, concentrically arranged and alternately developed. Lateral tubes, well developed at certain levels, may be stellate and link autotubes.

Remarks.—*Milleporidium* and *Steineria* are linked by the similarity of the general build of the coenosteum, and by the occurrence in both of coarse and fine-textured latilamellae and concentrically arranged short wide autotubes. They differ since *Steineria* has well developed lateral tubes, a difference which justifies generic separa-

tion. A genus which also has well developed lateral tubes is *Steinerella*.* This, however, has long wide autotubes and lacks the marked latilamellation of *Steineria* from which it is therefore generically separate.

Family allocation.—Genera characterized by wide and narrow autotubes thus include *Milleporidium* and *Promillepora*, in which lateral tubes are absent or subordinate, and *Steinerella* and *Steineria*, in which lateral tubes are a marked feature. This distinction, however, is not a clear cut one and the link between them due to the characteristic autotubes is such that they can justifiably be included in the one family, the Milleporidiidae.

STEINERIA ROMANICA (Dehorne), 1918
Pl. 75, figs. 1–4,9,10; Text-fig.2–5

Stromatopora romanica Dehorne, 1918, p. 221.
Stromatopora milleporoides (in part), *Stromatopora milleporoides* var. *romanica*, *Stromatopora romanica*, DEHORNE, 1920, p. 86–88, pl. 5, fig. 7 (not fig. 8), pl. 13, figs. 4,5.
Stromatopora milleporoides de *romanica* DEHORNE, 1923, p. 19; not *Stromatopora milleporoides*, p. 18.
Milleporidium milleporoides, KÜHN, 1927, p. 551; 1928, p. 87.
Milleporidium romanicum, ZUFFARDI-COMERCI, 1931, p. 71.
Stromatopora milleporoïdes, STEINER, 1932, p. 82.
Stromatoporina romanica, LECOMPTE, 1952, p. 21.

Synonymy.—There has been considerable confusion, partly due to the delay in publication (see Hudson, 1955b) of Dehorne's paper in the Com. Serv. Geol. Portugal, as to the validity of the species (or subspecies) names "*romanica*" and "*lusitanica*". The former species was founded by Dehorne in 1918, with a short but sufficient description based on a specimen from Roumania but with no figures in illustration and no designation of type specimens. In 1920 that author redescribed it, widening its connotation to include an undescribed form from the Lusitanian of Portugal which she made a "var. *lusitanica*," thus automatically recognizing a type "var. *romanica*." At the same time she suggested the substitution of the name *milleporoides* for the specific name *romanica*, an invalid substitution for the names are synonyms. The two varieties, which were both figured and localized, thus remained as *Stromatopora romanica* Dehorne, 1918, var. *romanica* Dehorne, 1918, and *Stromatopora romanica* Dehorne, 1918, var. *lusitanica* Dehorne, 1920. In Dehorne 1923, *Stromatopora milleporoides* was stated to be a new species, including "var. *lusitanica*" and "var. *romanica*," the type this time being "var. *lusitanica*," all of which was unnecessary and invalid. In 1931, Zuffardi-Comerci gave the two specific rank and subsequently this practice has been usually followed, the name "*milleporoides*" often being allocated sometimes to the one, sometimes to the other.

Lectotype (chosen Lecompte, 1952, p. 21).—Specimen 27 (Dehorne, 1920, pl. 5, fig. 7), and thin sections 27a-g cut from it; Stromatoporoid collection, Geological Laboratory, Sorbonne, Paris, from Upper Jurassic (?Lusitanian) of the Dobrogea, Roumania. This specimen consists of an aggregate of coenosteal columns each formed by a pair of joined proliferations. The three main columns, here referred to as A, B, C, are positioned in Dehorne's figure (1920, fig. 7, pl. 5) as follows: A, upper left; B, upper right; C, lower right. The figured surfaces and sections cut from these columns are, in order of position, as follows:

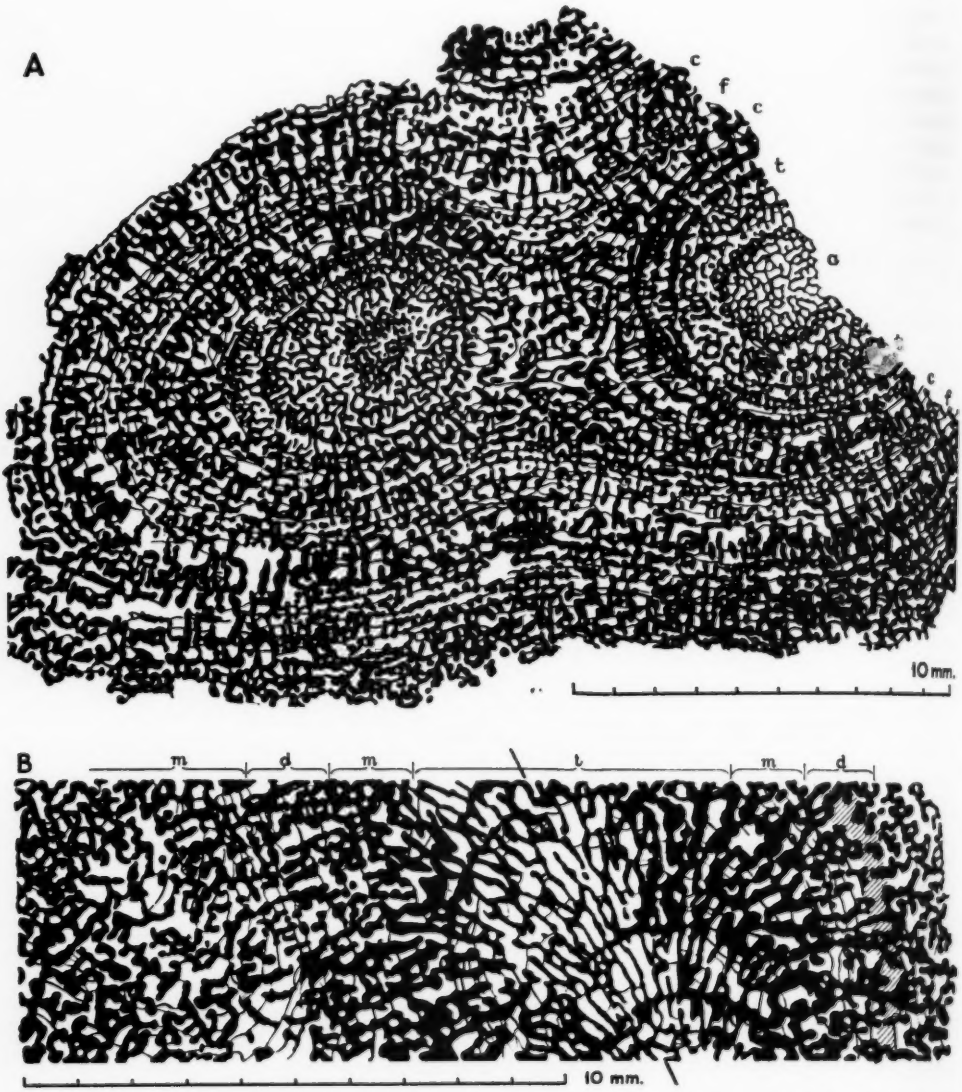
Column A: Thin section (now lost) of the upper proliferation (Dehorne, 1920, Pl. 13, fig.5); five longitudinal sections, 27b-f, cut from a thick transverse slice of the lower proliferation and here figured as Text-fig. 4

* *Steinerella* Lecompte, 1952 (type species: *Stromatopora mecosola* Steiner, 1932; lectotype: specimen A, figured Steiner, 1932, pl. 8, fig. 1,2, pl. 9, fig. 1, pl. 14, fig. 1, Valanginian, Ste.-Croix, Jura) was allocated by Lecompte (1952) to the Milleporellidae Yabe and Sugiyama, 1935. This allocation is an error since it ignores the occurrence in *Steinerella* of antotubes, fundamental structures not present in *Milleporella* Deninger, 1906, or any of the other genera usually allocated to the Milleporellidae. In *Steinerella*, as in *Milleporidium*, the wide autotubes proceed from narrow autotubes which may originate in or adjacent to the axial reticulum, and in *Steinerella loxola* (Steiner), 1932, certain of the wide autotubes are concentrically arranged, another characteristic feature of *Milleporidium*. The main difference between *Steinerella* and *Milleporidium* is that, in the former, lateral tubes are a marked feature both in the reticulum and on the coenosteal surface, whereas in the latter they are very subordinate. Nevertheless their occurrence in *Milleporidium* links the two genera and *Steinerella* is a member of the Milleporidiidae.

(27b, tangential section), Pl. 75, fig. 9 (27c, intermediate section), Text-fig. 2b (27b, axial section), Pl. 75, fig. 10 (27e, intermediate section), Text-fig. 5 (27f, tangential section); polished transverse surface (Pl. 75, fig. 2).

Column B: Polished surfaces (Pl. 75, figs. 3, 4).

Column C: Polished transverse surface (Dehorne, 1920, Pl. 13, fig. 4); transverse thin section 2g (Text-fig. 2a); polished transverse surface (Pl. 75, fig. 1).

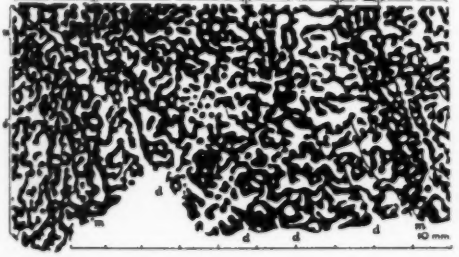


TEXT-FIG. 2—*Steineria romanica* (Dehorne). Outline diagrams of thin sections of lectotype, specimen 27 (see text). Line hachuring represents mud layers. *A*, part of transverse section 27g from column C showing (a) axial, (t) transitional, (c) coarse-textured and (f) fine-textured reticula. Section adjacent to that of Pl. 75, fig. 1. *B*, slightly oblique longitudinal axial section 27d from column A showing (t) transitional, (m) fine-textured, (d) coarse-textured dimorphic peripheral reticula.

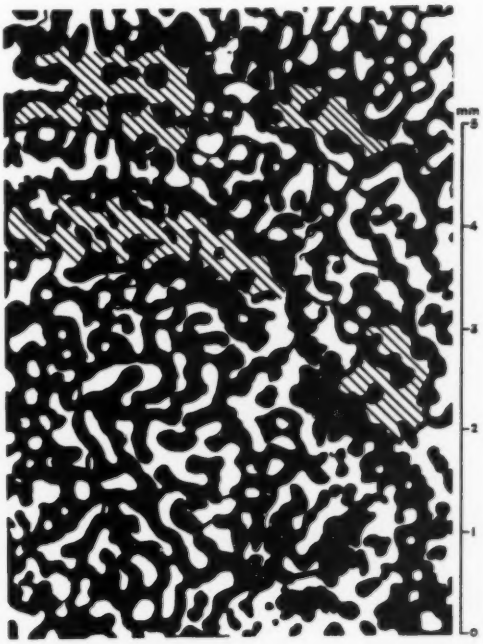
TEXT-FIG. *3*—*Steineria romanica* (Dehorne). Outline diagram of transverse thin section 27a of lectotype, showing central part of a columnar proliferation with narrow autotubes, and (a) axial, (t) transitional, (f) fine-textured and (c) coarse-textured reticula. Tabulae not shown.

The position of transverse section 27a (Text-fig. 3), cut by Lecompte from the lectotype, is not known; it is the central part of a proliferation near its origin. The section figured by Dehorne in 1920 as Pl. 14, fig. 2, has not been seen and its provenance is not known.

Diagnosis.—*Steineria* of paired columnar coenostea. Axial and peripheral reticula, the latter with alternate coarse and fine-textured latilamellae. Coenosteal-tubules, about 0.1 mm. to 0.15 mm. across, transversely circular, or elongate and tortuous, with walls about 0.1 mm. to 0.15 mm. thick. Transverse lamellae and tabulae well developed in fine-textured reticulum, the latter often forming extensive independent laminae. Wide and narrow autotubes respectively 0.25 mm. and 0.12 mm. across. Lateral tubes well developed at certain levels.

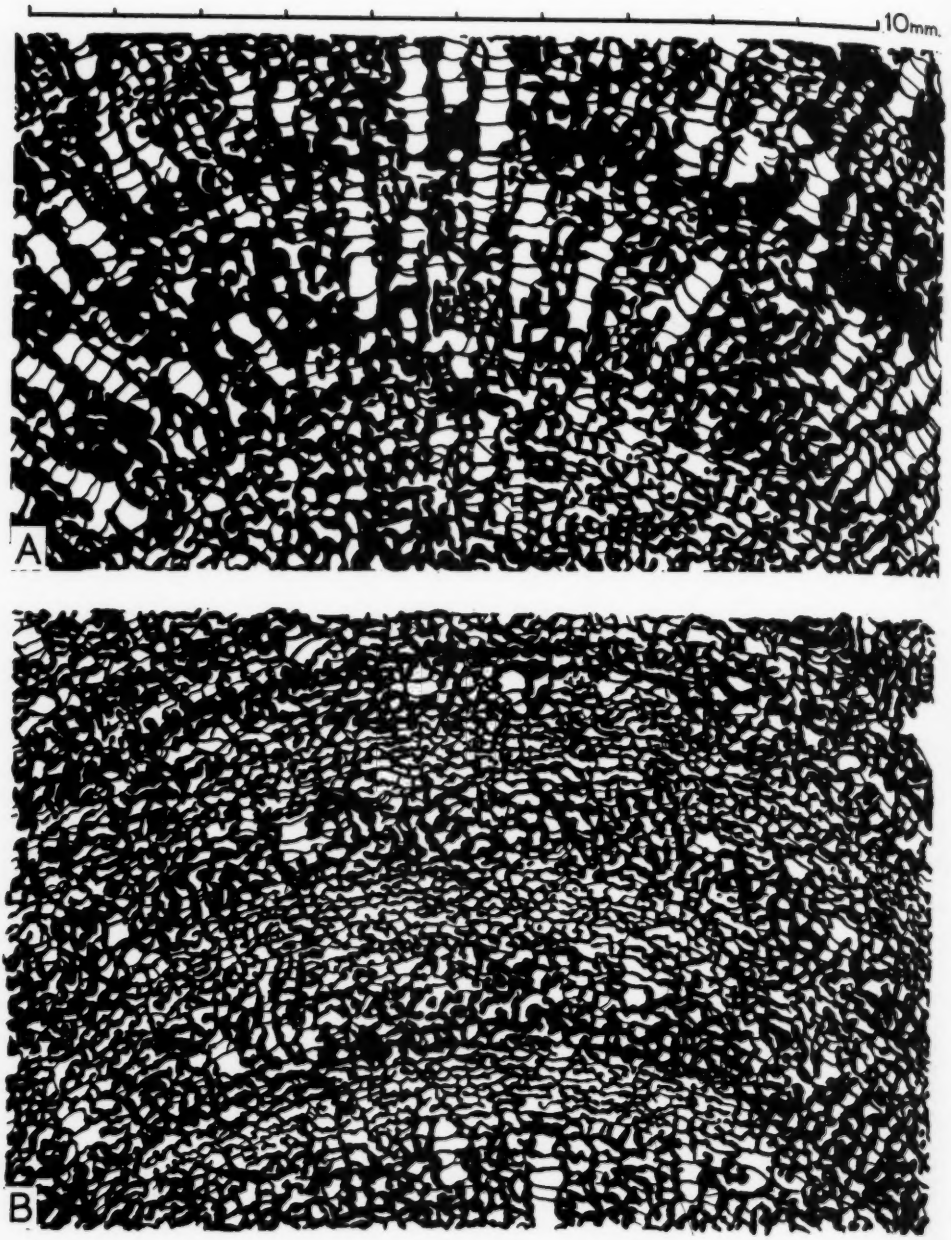


TEXT-FIG. *4*—*Steineria romanica* (Dehorne). Thin section 27b from column C of lectotype, tangential in centre and oblique radial at sides, showing (m) fine-textured monomorphic and (d) coarse-textured dimorphic reticula.



TEXT-FIG. *5*—*Steineria romanica* (Dehorne). Thin section 27f from column C of lectotype, lower part tangential and showing radial arrangement of lateral tubes in coarse-textured reticulum.

Description.—An irregular aggregate of stumpy coenosteal columns (Dehorne, 1920, pl. 5, fig. 7), each formed of a pair of proliferations (Dehorne, 1920, Pl. 13, fig. 4). Basal nodule not known. Surface with either a coarse vermiculate or fine-textured tubular mesh, the former with distinct circular autotube ostea and occasional lateral canals. Axial and peripheral reticula (Pl. 75, fig. 1, 4) formed of vertical lamellae, subordinate transverse lamellae and tabulae, the latter often continuous as extensive concentric



TEXT-FIG. *6*—*Promillepora kurnubi*, n. sp. Outline diagram of parts of thin section H 4898a (figured as Pl. 77, fig. 5), showing variation in peripheral reticulum of proportion of fine and coarse-textured latilamellae and number and length of autotubes.

laminae (Text-fig. 2a). The skeletal tissue of the lamellae consists of fine calcareous fibers radiating outwards and upwards from a central axis or plane: that of the tabulae is granular. Axial reticulum consists of sparsely tabulate vertical tubules (Text-fig. 2b) about 0.2 mm. across with walls about 0.05 mm. thick, mainly, in transverse section, irregular polygonal and elongate. In outer part (transitional to peripheral reticulum) tubules curve outwards and are crossed by thicker, aligned, and parallel transverse lamellae (Pl. 75, fig. 1 and Text-fig. 2b). Peripheral reticulum markedly latilamellate (Pl. 75, fig. 1,4) with alternate coarse and fine-textured reticula: in the former the vertical elements are dominant; in the latter the vertical and transverse elements are equally developed (Pl. 75, fig. 1,4). Vertical lamellae in the peripheral reticulum are continuous though slightly irregular. In the coarse-textured reticulum they are from 0.1 mm. to 0.15 mm. thick and transversely vermiculate, enclosing interspaces which may be circular but are generally elongate and tortuous and approximately the same width as the lamellae. In the fine-textured latilamellae, the vertical lamellae, about 0.1 mm. thick, enclose tubules approximately circular and 0.1 mm. across (Pl. 75, fig. 3). They are crossed by tabulae, often aligned and sometimes free for some distance, thus forming continuous, parallel, concentric laminae (Text-fig. 2a). Along these laminae, the vertical lamellae are often thickened and sometimes in contact, forming aligned transverse lamellae, about 0.2 mm. thick, and about the same distance apart.

Autotubes occur throughout the peripheral reticulum and contribute to the latilamellation since the autotubes of wide diameter occur mainly, though far from entirely, in the coarse-textured latilamellae and those of narrow diameter in the fine-textured, the wide autotubes being more common in the outer latilamellae (Pl. 75, fig. 1–4). These are of fairly constant width, generally about 0.25 mm. but occurring up to 0.35 mm. This marked difference in diameter from the surrounding coenosteal-tubules gives, in longitudinal and transverse sections, a dimorphic character to the reticulum of the coarser latilamellae (Pl. 75, fig. 1,4). In tangential sections (Pl. 75, fig. 3) the wide autotubes are seen to be rarely completely enclosed, since in most cases a small break in the walls of each communicates with the coenosteal-tubules. The narrow autotubes also have a fairly constant width of about 0.12 mm. (Pl. 75, fig. 4). As such they are not readily distinguishable from the coenosteal-tubules and with them they form a monomorphic reticulum. Transition from the one width to the other is rapid. Both wide and narrow tubules are closely tabulate, the tabulae never being thickened. This and their more continuous and straighter walls are a marked aid to their recognition especially on polished surfaces (Pl. 75, fig. 1–4).

Autotubes are initiated in the axial reticulum as narrow straight-sided tubes (Text-fig. 3). Wide autotubes of normal width occur in the first coarse-textured latilamellae.

Tangential sections of the dimorphic reticulum vary considerably owing to the occurrence or absence of lateral tubes. These are shallow tubules joining two or three autotubes and often connected by the coenosteal interspaces to other autotubes or to other lateral tubes (Pl. 75, fig. 3). Though their width is not constant it tends to be slightly less than that of the wide autotubes they envelope. These lateral tubes tend to occur at individual levels usually at the base of the dimorphic reticulum and to be radially grouped (Text-fig. 5). In transverse thin sections the autotubes and the connecting lateral tubes cannot be distinguished: on transverse polished surfaces the greater depth of the autotubes contrasts with the shallower depth of the lateral tubes (Pl. 75, fig. 3).

New proliferations are initiated by the outward extension of the reticulum of the coarse-textured latilamella immediately surrounding the axial reticulum (Pl. 75, fig. 2). The neighboring peripheral reticulum is thus divided, the two divisions gradually becoming concentrically arranged and forming new proliferations parallel to the original one.

STEINERIA SOMALIENSIS (Zuffardi-Comerci), 1931
Pl. 77, fig. 1, 2

Milleporidium somaliense ZUFFARDI-COMERCI, 1931, p. 70, text-figs. 10,11; 1938, p. 7, pl. 1,

figs. 5a,b; WELLS, 1943, p. 51, pl. 9, fig. 8; HUDSON, 1954b, p. 219, pl. 7, fig. 1a–c, pl. 8, fig. 3a,b; 1955b, p. 5.

Lectotype (here chosen).—Specimen figured by Zuffardi-Comerci, 1931, text-figs. 10,11. From Oolitico medio, bed b, of Bur Budulca, Uddur Plateau, southern Somaliland. Lusitanian-Kimmeridgian.

Middle East material.—H 4897 (1 piece) and thin sections a (Pl. 77, fig. 1) and b (Pl. 77, fig. 2). Upper Jurassic, Kurnub, Israel. Also Central and Southern Arabia (Hudson, 1954b, 1955b).

Diagnosis.—Coenosteum lamellar, with, on upper surface, short cylindrical proliferations with axial and peripheral reticula, the latter irregularly latilamellate. Latilamellae mainly coarse-textured with vertical and transverse lamellae irregular and discontinuous forming in vertical section a loose reticulate network, in which vertical lamellae are dominant. Transverse latilamellae and tabulae more common and interspaces smaller in fine-textured latilamellae. Wide autotubes short and approximately concentrically distributed in open-textured reticulum.

Description.—Coenosteum lamellar and ?encrusting, with short slender columnar proliferations, about 10 mm. to 15 mm. (commonly 12 mm.) in diameter, joined or free, and each with one or two axes of growth. Coenosteum of axial and peripheral reticula, the latter with irregularly alternate fine compact and coarse open-textured latilamellae, the latter forming greater part of reticulum. Vertical and transverse lamellae roughly at right-angles but irregular and discontinuous and hence irregularly reticulate in radial section. Constituent pillars and joining lamellae distinguishable. Vertical lamellae dominant, about 0.05 mm. to 0.1 mm. thick in axial reticulum and about 0.1 mm. to 0.2 mm. in peripheral reticulum and dominant in coarse-textured latilamellae. Coenosteal-tubules variable in diameter but generally from 0.1 mm. to 0.2 mm. across. Vertical lamellae more discontinuous in fine-textured latilamellae where tabulae and transverse lamellae are more common and interspaces smaller. Wide autotubes short, generally 1 mm. long but extend to 2 mm., about 0.3 mm. to 0.4 mm. across, and approximately concentrically distributed in open-textured reticulum. Narrow autotubes generally 0.15 mm. to 0.2 mm. across. Lateral tubes variable in form and size, sporadically distributed and not markedly differentiated. Tabulae may be aligned and are sometimes free and continuous, forming tabulate laminae. Skeletal tissue fibrous radiating outwards and upwards from a central axis or medial plane.

Generic allocation.—The pattern and texture of the coenosteal reticulum of "*somaliense*" differs from that of *Milleporidium* in which the vertical lamellae are straighter and more dominant. Its coarse-textured reticulum is, however, not unlike that of *Steineria romanica* and though "*somaliense*" lacks the regular latilamellation of that species since the fine-textured latilamellae which are such a feature of that form are but imperfectly represented in "*somaliense*," both species have the important diagnostic structures of lateral tubes and short and concentrically arranged wide autotubes and are therefore considered to be co-generic. The general pattern of the reticulum of *Steineria somaliensis* and the character of the coarse and fine-textured latilamellae have considerable resemblance to that of *Promillepora kurnubi* and it is possible that the two are closely related. As *P. kurnubi* is structurally more advanced than *P. pervinquieri* it is possible that these two species, *Steineria somaliensis*, and *S. romanica* are a morphological series illustrating the structural development of the Milleporidiidae from non-latilamellate to latilamellate forms with the development of fine-textured reticula in which transverse lamellae become more important.

Genus SHUQRAIA Hudson, 1954b

Type species (original designation).—*Milleporidium zuffardiae* Wells, 1943. Upper Jurassic; Ethiopia, Somaliland, southern Arabia.

Other species.—*Shuqraia arrabidensis* (Dehorne), 1920, emend. Hudson, 1955c; *Shuqraia arabica* Hudson, 1954b; *Shuqraia heybroeki* Hudson, 1954b.

Diagnosis.—Milleporidiidae with axial and peripheral coenosteal-reticula, the latter with dominant and fairly regular and

continuous vertical lamellae, and subordinate transverse lamellae, forming a vermiculate tubular reticulum. Narrow autotubes only. Lateral tubes, narrow and radially grouped, may be present.

Family allocation.—In his original description of *Shuqraia*, the author (1954b) allocated it to the family Stromatoporinidae basing his appreciation of that family on the redescription of *Stromatoporina* Kühn by Lecompte (1952) and the inclusion in it by that author of the species "*arrabidensis*," "*romanica*," and "*douvillei*." The two last of these species have, in this paper, been allocated to the Milleporidiidae on the basis of the occurrence, as in *Milleporidium*, of wide autotubes within the coenosteal-reticulum. The genus *Stromatoporina* has been redescribed (Hudson, 1955a) and however wide the definition of the Stromatoporinidae, the family based on it, is made, *Shuqraia* cannot be reasonably included in it. Nor, at first sight, can *Shquraia* be included in the Milleporidiidae since it does not possess the wide autotubes characteristic of *Milleporidium*. Such structures are, however, extensions from narrow autotubes and these have now been recognized in all species of *Shuqraia*. Lateral tubes, another characteristic structure in the Milleporidiidae, occur sporadically in *Shuqraia* notably in *S. arabica* Hudson, 1954b, and related forms (Hudson, 1955a). The genus is, therefore, structurally closely linked to the various genera of the Milleporidiidae and can be justifiably included in that family.

Genus SPORADOPORIDIUM Germovšek, 1954

Type species (by monotypy).—*Sporadoporidium rakoveci* Germovšek, 1954. Upper Jurassic (mainly Tithonian); Mackovec, near Novo Mesto, Slovenia, N. W. Jugoslavia.

Other species.—*Sporadoporidium libanoticum* (Hudson) described as *Milleporidium libanoticum* Hudson, 1954a. Calcaires à *Cidaris glandaria* (Kimmeridgian-Sequanian), Toumatt Djezzine, Lebanon.

Diagnosis.—Milleporidiidae with regular, generally continuous, vertical lamellae and subordinate transverse lamellae forming a vermiculately tubular coenosteal-reticulum, axial and peripheral. Tabulae few. Autotubes abundant, regular, tabulate and distinctly wide and narrow. Lateral tubes common, wide and radially arranged.

Family allocation.—Germovšek (1954) in his definition of this genus remarked on its similarity to *Milleporidium* but thought the presence of the structures here noted as lateral tubes precluded it from being classed in the Milleporidiidae and therefore created for it a new family the Sporadoporidiidae. It has been shown, however, that lateral tubes do occur in *Milleporidium* and there is therefore no reason to exclude it from the family based on that genus.

Genus MYRIOPORINA Kühn, 1939

Myriopora VOLZ, 1904, p. 103; 1913, p. 753; KÜHN, 1928, p. 87; YABE & SUGIYAMA, 1953, p. 157.

not *Myriopora* REUSS, 1846 (= *Myriapora* BLAINVILLE, 1830).

Myrioporina KÜHN, 1939, p. 34; ALLOITEAU *in* Piveteau, 1952, p. 382.

Type species (by monotypy).—*Myriopora verbeeki* Volz, 1904. Upper Jurassic, West Sumatra.

Diagnosis.—Milleporidiidae of regular, discontinuous, vertical lamellae and subordinate transverse lamellae forming a latilamellate reticulum of alternate vermiculate and regular, approximately circular, coenosteal-tubules, transverse lamellae well-developed in the former. Narrow autotubes mainly in fine-textured latilamellae. Lateral tubes narrow, well developed at intervals, generally at base of latilamellae, and often radially grouped around autotubes. Tabulae abundant, often aligned and independent.

Remarks.—Although the author has not been able to examine the holotype or topotypes of *M. verbeeki* (Volz), the excellent description and figures of Volz (1904, 1913) leave no doubt that Kühn (1939) and Alloiteau (1952) were correct in allocating the genus to the Milleporidiidae. The general pattern of the coenosteal reticulum of *Myrioporina* with its alternation of vermiculate and regular coenosteal-tubules is not unlike those of *Milleporidium* and *Steineria* and like the latter *Myrioporina* has marked lateral tubes at or near the top of the vermiculate reticula. Unlike these genera, however, its autotubes are not dimorphic, being of

the narrow type only, approximately of the same diameter as the coenosteal-tubules. In this it is comparable to *Shuqraia* and might have the same relationship to *Milleporidium*, as *Shuqraia* has to *Promillepora*.

REFERENCES

ALLOITEAU, J., 1952, Classe des Hydrozoaires, p. 377–398, *in* J. Piveteau, Traité de Paléontologie, vol. 1. Paris.

BALL, M. W., & BALL, D., 1953, Oil Prospects in Israel: Am. Assoc. Petrol. Geol. Bull., vol. 37, p. 1–113.

DEHORNE, Y., 1918, Sur les analogies de la forme branchue chez les Polypiers constructeurs des récifs actuels avec celle des Stromatopores des terrains secondaires: Comptes Rendus Acad. Sci., vol. 166, p. 219–222. Paris.

——, 1920, Les stromatoporoïdes des terrains secondaires: Mém. cart. géol. det. France, p. 1–170. Paris.

——, 1923, Stromatoporidés jurassiques du Portugal: Comm. Serv. Geol. Portugal, vol. 13, p. 12–21.

GERMOVŠEK, C., 1954, Les Hydrozoa du Jura supérieur aux environs de Novo Mesto: Acad. Sci. Art. Sloven., Class IV, Hist. nat. Ljubljana Razpr., vol. 2, p. 341–386.

HUDSON, R. G. S., 1954a, Jurassic stromatoporoids from the Lebanon: Jour. Paleont., vol. 28, p. 657–661.

——, 1954b, Jurassic stromatoporoids from southern Arabia: Notes Mém. Moyen-Orient, vol. 5, p. 207–221. Paris.

——, 1955a, Sequanian stromatoporoids from southwest Arabia: Notes Mém. Moyen-Orient, vol. 6, p. 225–241. Paris.

——, 1955b, On the Jurassic stromatoporoids: I. The type of *Stromatopora douvillei* Dehorne. II. *Milleporidium* and "*Stromatopora*" from Central Arabia: Ann. Mag. Nat. Hist., ser. 12, vol. 8, p. 13–20.

——, 1955c, On the Jurassic stromatoporoids: III. *Stromatopora arrabidensis* Dehorne: Ann. Mag. Nat. Hist., ser. 12, vol. 8.

KÜHN, O., 1927, Zur Systematik und Nomenklatur der Stromatoporen: Centralblatt Min. Pal. Geol., Abt. B, vol. 12, p. 546–552, Stuttgart.

——, 1928, Hydrozoa: Fossilium Catalogus, I (Animalia), pt. 36, 2, Mesozoicum, p. 76–94. Berlin.

——, 1939, Hydrozoa: *in* O. H. Schindewolf, Handbuch der Paläozoologie, vol. 2a, pt. 5, p. 1–68. Berlin.

LECOMPTE, M., 1952, Révision des Stromatoporoïdes Mesozoïques de Collections Dehorne et Steiner: Bull. Inst. roy. Sci. nat. Belgique, vol. 28, no. 53, p. 1–39.

REMEŠ, M., 1905, Fauna der sog. exotischen Blöcke des Stramberger Kalksteins in Ryachalitz (Mähren): Bull. internat. Acad. Sci. Emp. F.J.I.: Cl. Sci. Math. Nat. Med., 10th year, p. 33–37. Prague.

STEINER, A., 1932, Contribution à l'étude des Stromatopores secondaires: Mém. Soc. Vaudoise sci. nat., vol. 14, p. 105–201, *and* Bull. Lab. Geol. Univ. Lausanne, no. 50, p. 1–117.

STEINMANN, G., 1903a, *Milleporidium*, eine Hydrocoralline aus dem Tithon von Stramberg: Beitr. zur Paläontologie und Geologie Oesterreich-Ungarns und des Orients, vol. 14, p. 1–8. Vienna.

——, 1903b, Einführung in die Paläontologie. Leipzig.

——, 1907, Einführung in die Palaontologie. 2nd ed. Leipzig.

WELLS, J. W., 1943, Palaeontology of the Harrar Province, Ethiopia. Pt. 3. Jurassic Anthozoa and Hydrozoa: Am. Mus. Nat. Hist. Bull., vol. 82, p. 31–54.

WIENER, G., 1955, Geology and mineral deposits of Makhtesh Hathira (Southern Israel): Swiss. Ass. Pet.-Geol. & Eng. Bull., vol. 21, no. 61, p. 41–56.

YABE, H., & SUGIYAMA, T., 1935, Jurassic stromatoporoids from Japan: Tôhoku Imp. Univ. Sci., Rept. ser. 2 (Geol.), vol. 14, p. 135–192.

——, & TOYAMA, S., 1927, *Milleporidium remesi* Steinmann? from the Torinosu Limestone of Itsukaichi, Province of Musashi: Jap. Jour. Geol. Geog., vol. 5, p. 117–119. Tokyo.

ZUFFARDI-COMERCI, R., 1930, Sulle faune del sopracretacico in Puglia con particolare reguardo a quella di S. Cesarea: Boll. R. Ufficio geologico Italia, vol. 55, no. 7, p. 1–35.

——, 1931, Corallari e idrozoi del Giuralias della Somalia: Paleont. Italica, vol. 32, p. 49–75.

——, 1938, Corallari e idrozoi giurassici dell' Ogaden (A.O.I.): Palaeont. Italica, vol. 32, suppl. 3, p. 1–9.

MANUSCRIPT RECEIVED OCTOBER 29, 1955

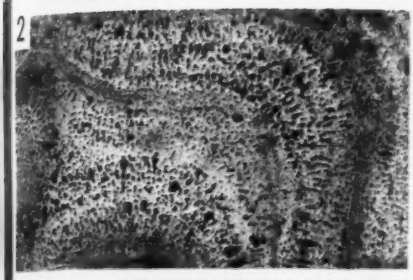
EXPLANATION OF PLATE 77

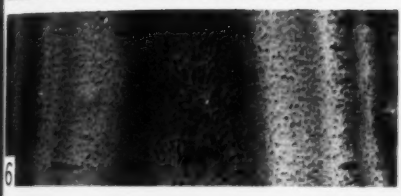
All from Kurnub Limestone (Upper Jurassic), Maktesh Hathira, southeast of Beersheba, northern Negev, Israel. All photographed by reflected light.

FIG. *1,2*—*Steineria somaliensis* (Zuffardi-Comerci). Serial transverse thin sections of H 4897a and b. *1*, ×3.5; *2*, ×4.3. (p. 727)

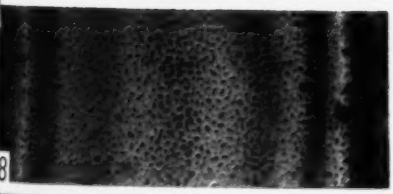
3-11—*Promillepora kurnubi*, n. sp. *3,4*, longitudinal axial and transverse thin sections, ×4.6, of immature coenosteal columns of paratypes H4901a and H4900a. *5*, transverse thin section, ×3.5, of holotype H 4898a. *6–11*, longitudinal surfaces, ×3.8, of immature coenosteal columns of paratype H 4902. Surfaces serial from *6*, axial, to *11*, tangential near surface. (p. 721)

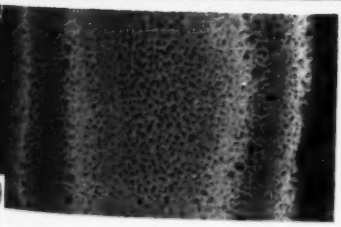
1

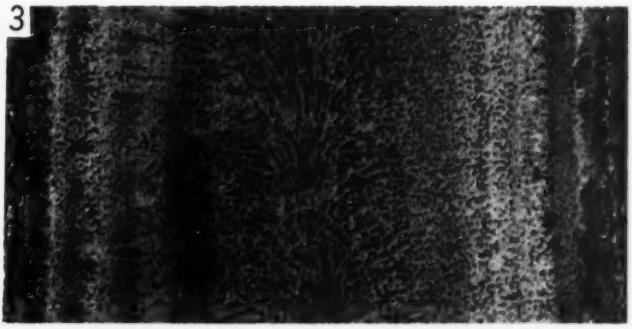

2

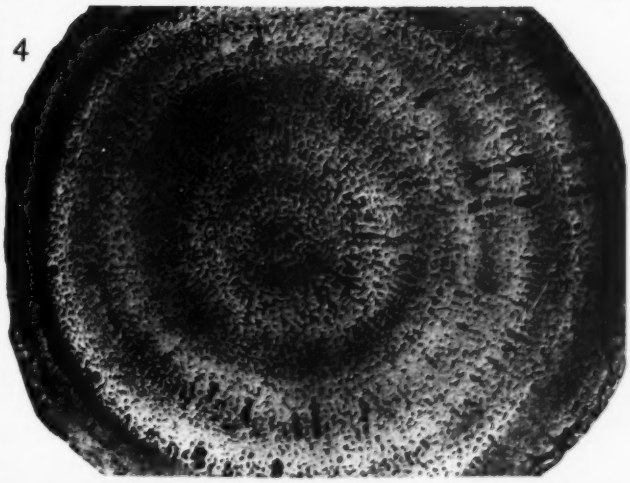

6

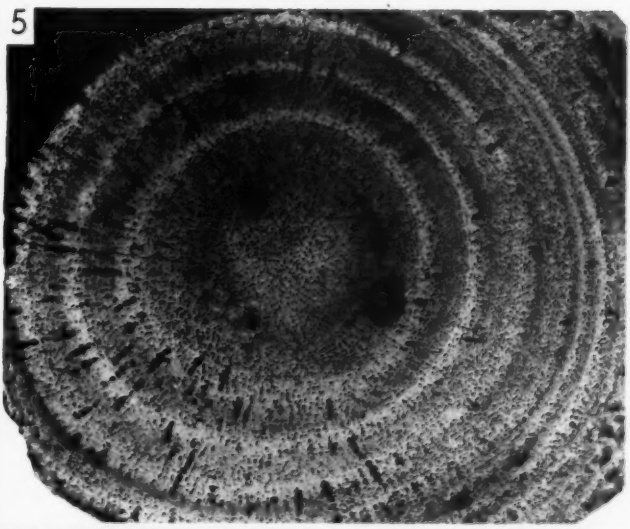
7

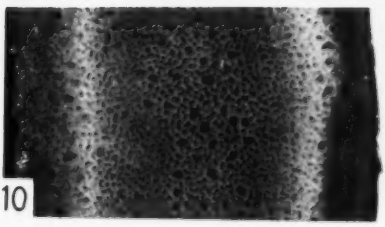

8

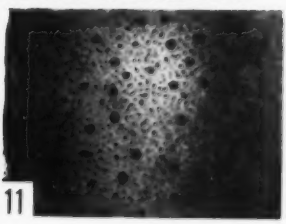

9


3


4

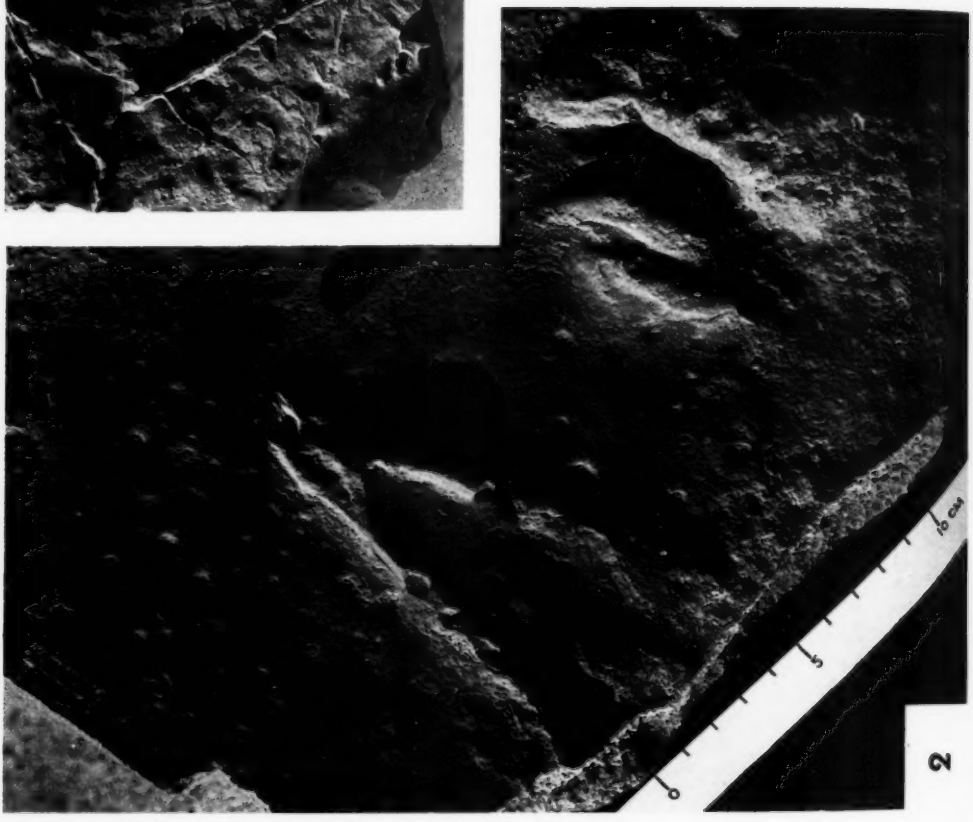

5


10


11

1

3


2

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 731–740, PL. 78–80, MAY 1956

ICHNITES FROM THE TRIASSIC MOENKOPI FORMATION OF ARIZONA AND UTAH

FRANK E. PEABODY
Department of Zoology, University of California, Los Angeles

ABSTRACT—A miscellaneous collection of ichnites from the Triassic, mostly from the Moenkopi formation, includes: a trackway of *Chirotherium coltoni* hitherto known from a single set of impressions, isolated manus impressions of *C. moquiense* from Utah and Arizona, a mudflat impression thought to be of an archosaur palate, rotodactylid and lacertoid trackways from Utah, "swim" tracks of tetrapods indicating pool environment from Utah, and arthropod trails from Arizona and South Africa.

The chirotheriid and rotodactylid trackways of the Moenkopi in their distribution and stage of evolution support McKee's findings from physical data that the type Moenkopi formation of Arizona represents only the late part of total Moenkopi time.

INTRODUCTION

AN EXTENDED study of vertebrate trackways from the Moenkopi formation of Arizona and Utah was made in 1948 by the writer from existing collections. Since that time miscellaneous, additional material has accumulated which justified further description. Also, important geological work by Gregory (1948), Scott (1950), Poborski (1954) and especially by McKee (1954) on the far-flung exposures of the Moenkopi gives added significance to the many trackways and other impressions found on ancient mudflats preserved in this remarkable geologic formation. The present paper is part of a continuing program conducted by the Museum of Paleontology of the University of California and the Museum of Northern Arizona to study all the geological and paleontological aspects of the Moenkopi formation. New discoveries add to our information of the trackway genera *Chirotherium* and *Rotodactylus* and extend their known occurrence several hundred miles northward and also into intermediate regions. These particular trackways represent pseudosuchian reptiles with highly characteristic foot structure and as such are valuable guide fossils to the Triassic. Also of interest are impressions relating to the possible identity of the tetrapods making the trackways and to the paleoecology of Moenkopi time.

ACKNOWLEDGMENT

Drs. Charles L. Camp and Samuel P. Welles kindly granted the privilege of and facilities for describing most of the fossils treated here. Mr. Charles Kelley, custodian of Capitol Reef National Monument, and the first to discover *Rotodactylus* in this region, kindly supplied me with photographs and information on occurrence of footprints. Drs. Wann Langston and Donald Baird have kindly provided me with latex duplicates of certain of the trackways described here. Dr. Rober W. Wilson provided a critical reading of the manuscript.

EXPLANATION OF PLATE 78

FIG. *1*—Trackway of *Chirotherium coltoni;* Meteor Crater, Ariz.

2—Supposed impression of archosaur palate (left) associated with "swim" track (right); Meteor Crater, Ariz.

3—Isolated manus impressions (cast) of *Chirotherium* cf. *C. moquiense;* Wupatki National Monument, Ariz.

DESCRIPTIONS

CHIROTHERIID FOOTPRINTS

New occurrences of chirotheriid footprints are mainly of isolated specimens with the exception of a series of three consecutive steps of *Chirotherium coltoni*. The trackway pattern supplied by the latter specimen adds important data for the species, since the type is based on a single set of footprints. Of eight well-defined chirotheriid species from the Moenkopi only *C. rex* remains incomplete as concerns the trackway pattern, and this information is available whenever large scale excavation can be done at the type locality (Peabody, 1948, p. 380).

Family CHIROTHERIIDAE Abel
CHIROTHERIUM COLTONI Peabody

Chirotherium coltoni PEABODY, 1948, p. 385, fig. 30A, pl. 44A.

Type.—UCMP 37329.

Horizon and locality.—Lower part of Moenkopi (Wupatki member of McKee, 1954), near Meteor Crater, Arizona; UCMP loc. V3835 (Peabody, 1948, fig. 4b).

Diagnosis (Revised from Peabody, 1948, p. 385).—Small-manus chirotheriid with pes digit IV much shorter than III and slightly shorter than II; pes length 12.2 cm.; pes digit group I–IV relatively long and metatarsal pad on pes digit V relatively small; trackway pattern narrow with pace angulation of 165 degrees, ratio of pes length to stride 5.5 to 1, manus regularly emplaced farther forward of pes and with shallower impression than in other North American chirotheriids.

Discussion.—In 1951, Dr. Charles L. Camp of the University of California Museum of Paleontology revisited the type locality of *C. coltoni* and discovered a large slab (Pl. 78, fig. 1) 65 cm. in diameter which contained on its under surface three consecutive steps of this species. Since the species was based on a single set of footprints, the newly discovered trackway adds important detail. The trackway was found along the road at the same place (Peabody, 1948, fig. 4b) as the type specimen and had been turned up by workers on the highway while excavating in the side of a small, low butte. Similarity of the thickness of the slabs, of the appearance of shrinkage cracks on the cast surface, and of the details of the footprints thereon leave no reasonable doubt that the trackway of three consecutive steps represents the same individual that recorded the isolated set of footprints recovered in 1938. In all probability the type and the newly discovered specimens are part of the same trackway.

The trackway of *C. coltoni* proves to be narrow, as expected, having a pace angulation of 165 degrees, a stride of 67.8 cm. with digit I of manus and pes overlapping the midline of the trackway; the pes is turned outward 25 degrees (digit III as base line) from the midline. Stride length-pes length ratio is 5.5 to 1. As suggested by the type, the manus is remarkably shallow in its impression compared with the pes and the manus regularly falls well in advance of the pes—a distance greater than for any other chirotheriid of North America. Since there is nothing about the pes to indicate a rapid gait (and thus increased weight on the pes) one can conclude that *C. coltoni* is, as suspected, a species definitely farther advanced toward bipedality than species having a larger manus. This strengthens my original conclusion that since this species is a contemporary of primitive large-manus chirotheriids, there is no chronological series of Moenkopi species to demonstrate the evolution of small-manus from large-manus forms. Rather, the two kinds are contemporaneous in the Moenkopi and represent two well-defined divisions, probably of subfamily rank, of the Chirotheriidae. Also the lack of a demonstrable series of chirotheriid species in the type Moenkopi showing definite evolution of form fits better with McKee's view that the type Moenkopi represents only a small part of total Moenkopi time.

Chirotherium moquinense[1] Peabody
Pl. 78, fig. 3; Pl. 80, fig. 2

Chirotherium moquiensis PEABODY, 1948, p. 374, fig. 26, pl. 41,42D.

Type.—UCMP 37345, Pl. 80, fig. 2.

Horizon and locality.—UCMP loc. V4930. Approximately 30 feet below contact with Shinarump formation, in upper part of

[1] Dr. Donald Baird has kindly brought to notice incorrect endings used for three specific names by Peabody, 1948. Correct form is: *C. diabloense*, *C. cameronense* and *C. moquiense*.

Moenkopi beds (Upper red member of H.E. Gregory); southern Utah, 5 miles west of Navajo Wells on Kanab-Paria road and 2 miles south of road (S. P. Welles field notes, 1949, p. 634).

Diagnosis.—A giant chirotheriid of the large-manus group, with bulky foot structure and a reduced digit IV of the manus (see Peabody, 1948, p. 374).

Discussion.—An isolated cast of a manus impression found by S. P. Welles in 1951 east of Kanab is the second occurrence of a chirotheriid to be found in Utah. It occurs in the upper red member of the Moenkopi as do the Rockville specimens (Peabody, 1948, p. 378).

The left manus was shallowly impressed, approximately one centimeter deep, but deep enough to show the position of the five digits. However, digit V is only a rounded "punch mark," a characteristic peculiar to *C. moquinense* among Moenkopi species. There is no scale pattern evident, but digital pads show slight constrictions along lateral margins, a characteristic lacking in the other giant species *C. rex*. The claws on digits I-V were triangular; no claw is evident in the mark made by digit V. The overall size of the manus is the maximum known for Moenkopi species, but no larger than the manus of the Rockville specimen. Measurements of the manus are:

Width, overall of digits I–V	18.5 cm.
Width, overall of digits I–IV	15.0 cm.
Length of digit IV	8.0 cm.
Length of digit III	10.0 (est.)
Angle of digit I to IV	50 degrees
Angle of digit II to IV	35 degrees

The isolated manus might be mistaken for the pes of a primitive bipedal dinosaur such as *Plateosaurus*, but several considerations rule out this conclusion. The impression is too short anteroposteriorly, and the digits too divergent for the pes of either a chirotheriid or of a primitive bipedal dinosaur. Moreover, the impression is closely similar to others known to be the manus impressions of a species which characteristically records an abbreviated impression of manus digit V.

It is possible that the German species, *C. thuringiacum* (Lillienstern, 1938), is in reality based on manus impressions of a giant, large-manus chirotheriid rather than on any pes impression as assumed by Lillienstern, and also by Kuhn (1938).

In 1951, Superintendent Fred Brueck of the Wupatki National Monument northeast of Flagstaff, Arizona, showed me two specimens (Pl. 78, fig. 3) of manus impressions of a giant chirotheriid. The absence of digit I in an otherwise deeply impressed manus suggests *Chirotherium moquinense*. These specimens were found locally in the lower beds (Wupatki member of McKee) of the Moenkopi.

In passing it should be noted that Mr. Brueck has at the ranger station the alleged footprints of a giant chirotheriid found near Navajo Bridge on the Colorado River 80 miles north of Cameron, Arizona. The footprints are clearly artifacts being man-made engravings of human footprints in sandstone.

Supposed Impression of an Archosaurian Palate
Pl. 78, fig. 2

Specimen.—UCMP 4094.

A narrowly triangular impression, cast in sandy limestone, was found in 1938 approximately 2 feet above the mudflat surface which bore the trackway of *Chirotherium minus* (Peabody, 1948, fig. 16). The triangular impression (12 cm. long×6.5 cm. wide overall) is most deeply impressed anteriorly (i.e., at the apex of the triangle); its base is partly damaged by weathering.

The triangle has an unequally bifurcate apex with two concavities side by side. The sides of the triangle are raised ridges pierced on one side by a series of three evenly spaced rounded cavities; the anteriormost is 5 mm. long by 4 mm. wide. A single cavity appears in the opposite ridge and opposite the anteriormost cavity in the series of three; and there is faint suggestion of a second cavity posteriorly. The central area of the triangle is slightly raised, that is, at a different and lower level with respect to the surrounding surface of the original mudflat surface.

Most of the innumerable impressions found on Moenkopi mudflats may be explained reasonably (for example, the peculiar current crescents, Peabody, 1947), but the triangular impression lacks an explanation so far unless it represents the impres-

sion of the palate of a reptilian skull perhaps with portions of adhering, dried skin. There are a number of characteristics which make this conclusion reasonable.

The impression was made originally in the red mud but it is doubtful if the mud was ever exposed for long to the air—shrinkage cracks are lacking. Associated with the impression are skid marks (pl. 78, fig. 2) comparable to those described later which appear to be those of some aquatic tetrapod moving in a shallow pool. The triangular impression occurred at a level (Peabody, 1948, fig. 4a) within several feet stratigraphically and geographically of other levels which bear numerous footprints of *Rotodactylus* and *Chirotherium* and, not far away, osseous remains of varied labyrinthodonts. The impression cannot be a footprint of a vertebrate or invertebrate and is unlike any plant impression. The divergent ridges with a series of evenly splaced cavities clearly shown on one ridge with apparently matching cavities on the other ridge suggest very strongly the alveolar cavities in the jaw of some thecodont reptile. Either lower or upper jaw might be represented but the broad symphysial mass with paired, rounded concavities suggests a palate and hence upper jaws. The size of the impression, if a palate, is not much larger than *Euparkeria;* the size range of chirotheriids at nearly the same stratigraphic level and geographic locality more than encompasses the necessary dimensions were the palate of chirotheriid and/or of pseudosuchian origin.

On purely physical grounds it is entirely possible that a fragmentary, desiccated, reptilian skull which had lost the teeth could have been deposited by flotation in a shallow river pool in such a way as to leave an impression showing in fair detail the alveolar ridges and cavities. Vetebrate scavengers or the onset of renewed stream flow associated possibly with a short period of subaerial exposure could then have transported the object elsewhere leaving an impression to be filled and cast by the next overlying sediment.

If it be assumed that the impression represents the alveolar surface of a vertebrate jaw, a reptile rather than a fish or amphibian is indicated. The widely spaced and large alveolar cavities limited to the presumed cheek region immediately suggest a primitive, ornithischian archosaur. The snout end, although apparently broken off at the level of the premaxillaries, lacks the enlargement characteristic of therapsid reptiles and associated with enlarged caniniform teeth. (Olson & Beerbower, 1953, have described the lower jaw of a carnivorous therapsid from the Middle Permian of Texas.) The pair of large elongate cavities present in the snout are in the correct position to represent paired internal nares. The alveolar ridges converge evenly as in primitive archosaurs with no flaring evident in either the snout or post-maxillary region. The angle of convergence is 25 degrees, the same as in the lower jaw of a young modern crocodile, and about the same as comparable parts of the upper jaws of primitive archosaurs, for example, *Plateosaurus* 20 degrees, *Euparkeria* 25 degrees, *Eyrthrosuchus* 26 degrees, and the primitive diapsid *Youngina* 25 degrees (data from Romer, 1945, and W. K. Gregory, 1952). It seems clear that the impression, if that of a jaw, represents a fairly narrow jaw such as found in generalized archosaurs rather than in any forms with short, wide jaws or elongate, fish-catching jaws. We know from osseous remains that such narrow-jawed pseudosuchians existed

---

EXPLANATION OF PLATE 79

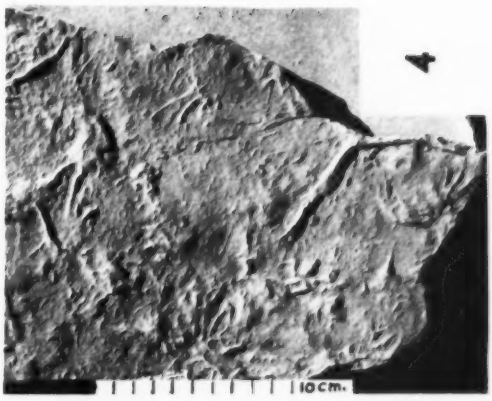
FIG. *1*—Portion of limestone lens (upside down) showing numerous cast impressions of "swim" tracks of tetrapods; Vernal, Utah.

2—Closeup, vertical view, of part of surface shown in fig. 1.

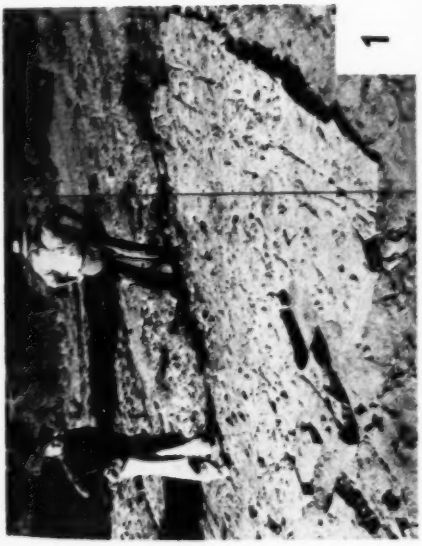
3—Slab of siltstone showing casts of "swim" tracks—some arranged in series (running left to right); Capitol Reef National Monument, Utah; Charles Kelly photo.

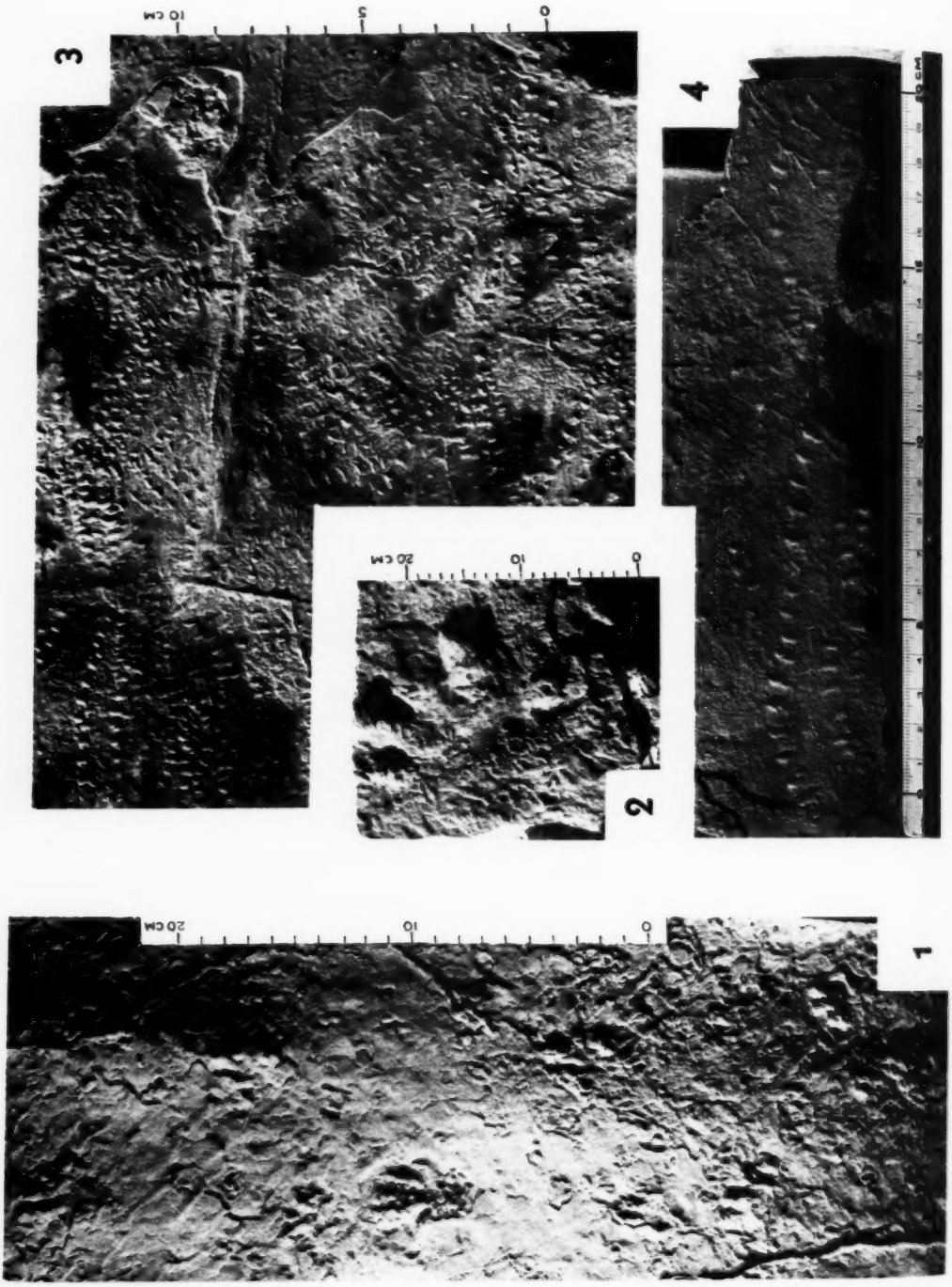
4—Lacertoid footpfints scattered on slab from Paria, Utah.

2


4
10cm.

3


1


3
10 CM
5
0
4
20 CM
2
20 CM
10
0
1
20 CM
10
0

in the Moenkopi, for example, *Arizonasaurus* (Welles, 1947), and the jaws of either *Chirotherium* or *Rotodactylus* in all probability were comparable. *Arizonasaurus* could conceivably represent a species of large chirotheriid. The clear indication in the impression of large, widely separated cheek teeth associated with an edentulous snout suggests some sort of primitive ornithischian.

The triangular impression is especially worth noting because a positive identification of the creator of the many pseudosuchian trackways in Triassic strata is yet to be made. The impression is the first which may indicate directly a body characteristic other than of the feet and tail and is closely associated with chirotheriid trackways. That at least some chirotheriids may have been herbivorous, pre-ornithischians is not unlikely. Indeed, the hoof-like structure of the manus of especially the giant chirotheriids and the broad, spatulate claws of the pes of certain species, for example, *Chirotherium rex*, suggest the possibility.

Non-chirotheriid Footprints
Pl. 80, fig. 1

Capitol Reef National Monument.—Identifiable trackways of *Rotodactylus** (Peabody, 1948, p. 325), a semibipedal pseudosuchian of small size, have been observed in the upper part (probably the upper red member of H. E. Gregory) of the Moenkopi formation near the west boundary of Capitol Reef National Monument, Utah. The locality is immediately north of the Fruita-Torrey road, 3.7 miles west of the headquarters building and was discovered by Mr. Charles Kelly, custodian of the Capitol Reef National Monument. This species of *Rotodactylus* as determined in the field is close to *R. mckeei* of the Hurricane, Utah, region, and is definitely not like the larger, more advanced *R. bradyi* of the Cameron, Arizona, region. Unfortunately, the specimens from Capitol Reef are not available for description at this time.

The general locality has produced various other vertebrate footprints and an excellent limuloid trackway in addition to "swim" tracks described below. These materials are in the possession of Mr. Kelly.

In 1953, a University of California field party collected a tetrapod trackway (UCMP loc. V5366, UCMP 43751, Pl. 80, fig. 1) from a point 100 yards up Sulphur Creek from the old lime kilns above the ranger station. The horizon is approximately 300 feet above the base of the Moenkopi and 175 feet above the Sinbad limestone member (thus presumably in the upper red member).

The trackway is shallowly impressed and thin exfoliations now damage the original impressions. A short description is worth while although a formal name is not given to the specimen.

A small tetrapod with pentadactyl manus and pes walked nearly straight across a mud surface bearing a faint pattern of shallow ripple marks. No tail mark is evident. In 15 consecutive steps preserved, the footprints are somewhat variable as to relative position and they definitely toe leftward (probably upslope as is usual with primitive tetrapods crossing obliquely a sloped surface).

The manus impression measures approximately 2.4 cm. wide by 2.6 cm. long, overall; the pes is 3.0 cm. wide by 3.8 cm. long, overall. These measurements vary somewhat from print to print because of variable bending of lateral digits. The average stride is 15 cm.; the pace angulation is 115 degrees maximum and averages 109 degrees for the

* Bock (1952, p. 422) does not demonstrate in any adequate way the synonymy of *Rotodactylus* with *Ichnium*. Also, his contention that the pes of living lizards may be elevated, as in *Rotodactylus*, to a digitigrade posture by a backwardly directed digit V is not in accord with the facts.

EXPLANATION OF PLATE 80

FIG. *1*—Trackway of ?amphibian (latex cast of original) from Capitol Reef National Monument, Utah.
2—Manus impression (cast) of *Chirotherium moquiense;* Kanab, Utah.
3—Arthropod trails (cast); Meteor Crater, Arizona.
4—Similar, but larger arthropod trail (cast); *Cynognathus* zone, Lower Triassic of South Africa.

normal walking pace (a momentary pause is evident at steps 11–12–13 resulting in a drop of pace angulation to 82 degrees minimum). The average position of consecutive pes impressions is 1.3 cm. from the midline of the trackway pattern, and the ratio of stride to pes length is 4 to 1. The manus regularly occurs about 2 cm. ahead of the pes, and in correlation with the "toe left" orientation of the feet, is displaced leftward with respect to the pattern of pes impressions. Also correlated with the sidling motion to the left is an outward curving of digit IV of the left pes (not shown in the normal print). Using digit III as the long axis of the foot, the right pes is turned out slightly (8 degrees max.) and the left pes is turned out much more (32 degrees max.); the right manus is turned well inward (25 degrees max.), the left manus slightly inward (8 degrees max.). These orientations, of course, indicate a sidling gait. In a symmetrical pattern the pes probably would be turned outward about 15 degrees, the manus about 10 degrees inward. The pentadactyl manus and pes are chirotheriid in general appearance. Digit IV is definitely longer than III and no claw marks are surely in evidence; the thumb-like digit V is set slightly forward of the chirotheriid position, and articular knobs are lacking on the fairly slender digits. The metapodial-phalangeal border of digit group I–IV is not sharply impressed.

Superficially the trackway appears to be that of a very primitive chirotheriid but many characters of the trackway pattern and of the feet make this conclusion unlikely. The stride, pace angulation, stride-pes length ratio are significantly less than in the most primitive Moenkopi chirotheriid, *Chirotherium diabloense;* the chirotheriid manus is smaller relative to the pes and is always turned out, never inward, and always has digit IV shorter than III (although pes digit IV may be longer than III); also the inter-pes distance is excessive. Lack of claw marks is probably significant here for all chirotheriids, no matter how small, show distinct claw marks. Also the chirotheriid thumb-like digit V is set farther back, and a definitive posterior border of digit group I–IV is apparent even in light impressions. The trackway is certainly not rotodactylid or lacertoid or even definitely reptilian. All characters considered, an amphibian of generalized body form may have made this trackway, although the footprints are not in the least like those of any living urodele, and the manus has five digits. [Current belief seems to be that the Amphibia characteristically have only four digits on the manus. While this may be true for the Urodela, Salientia and some labyrinthodonts, it is not proved as a constant character for Paleozoic amphibians. Anthracosaur amphibians (*Seymouria*) and undoubted amphibian footprints (*Hyloidichnus*) from Permian beds indicate that a five toed manus did exist and may have been more common than heretofore believed.]

Paria, Utah.—Lacertoid footprints resembling *Akropus* of the German Bunter were discovered in 1951 approximately 3 miles southwest of Paria on the south side of the Kanab road in a small ravine. According to C. L. Camp, the horizon is low in the Moenkopi section (presumably this means low in the upper red member, since at all other localities in southern and central Utah footprints occur only in this member). The occurrence of lacertoid tracks similar to those described from the Moenkopi of Arizona (Peabody, 1948) is of more than passing interest because similar tracks have been described from probably correlative strata in Wyoming (Lull, 1942; Branson, 1946). Although Lull refers certain of these Chugwater tracks to a Carboniferous genus and concludes that the strata are probably Permian, the similarity of his and Branson's material to Moenkopi and also to Bunter specimens from Germany (Lillienstern, 1939) is striking. Furthermore, the three-toed footprint occurring with Lull's Chugwater tracks is easily explained if the beds in question are Moenkopi correlatives. Three-toed tracks of bipedal dinosaurs associated with chirotheriids are known from the Bunter, a general correlative of the Moenkopi, and from the Upper Triassic of New Jersey (Baird, 1954). However, no such association has been found yet in the type Moenkopi.

Vernal, Utah.—In 1946 the University of California Museum of Paleontology investi-

gated thoroughly the Moenkopi formation exposed on the southeastern flank of the Uinta Mountain anticline in northeastern Utah. Although extensive surfaces bearing "swim" tracks are fairly common, subaerial tracks are exceedingly rare. One trackway of a small tetrapod (?reptile) showing an undulate tail mark was found in the lower beds exposed approximately 2 miles up an eastern tributary of Brush Creek north of Vernal. The trackway was preserved as a cast on the under surface of a stratum of massive mudstone and could not be collected readily.

Miscellaneous localities.—McKee (1954, table 16) notes localities where trackways of vertebrates have been found at other than those noted by Peabody (1948). Among the localities are several which I have not seen and from which apparently no material has been collected. McKee believes the trackways are reptilian (some may be subaquatic "swim" tracks). The localities are: Shinumo Altar, 12 miles northwest of Cameron; 2.5 miles northwest of Navajo Bridge; and Monument Valley (all in Arizona); Bears Ears and Lavender Canyon (Utah).

Further information on footprints from the Muddy Mountains of Nevada reported in passing by Longwell (1928) is now available. Dr. Donald Baird reports (personal communication) that of three small footprints (Yale Peabody Museum specimens) on reddish-brown shale from near the top of the Weiser limestone (Moenkopi), Muddy Mountains, YPM 3757 and 3758 represent a small amphibian; the other, YPM 3760, represents the trackway of a horseshoe crab. Latex molds (supplied by Dr. Baird) of the two original slabs show three similar sets of lightly impressed footprints; two of the sets seem to be consecutive. The footprints indicate a small, short-bodied tetrapod, probably amphibian, with blunt-ended, clawless digits, offset digit V on the pes, relatively small manus with only four digits apparent and with digit IV shorter than III, and a relatively long stride.

Subaqueous "Swim" Tracks of Tetrapods
Pl. 79, fig. 1–3

The most common impressions occurring in Moenkopi strata are what appear to be "swim" tracks of a tetrapod of about the size of large capitosaurid amphibians. These impressions are nearly always found preserved as casts on the under side of a lens of usually thin limestone and may cover an area exceeding a thousand square feet. Probably many casual references to "vertebrate tracks" in the Moenkopi allude to impressions of this nature. The best examples of such occurrences known to me are in the upper red member of the Moenkopi formation near the western boundary of Capitol Reef National Monument, Utah (Pl. 79, fig. 3; 2 miles west of the headquarters building on the south side of the Torrey-Fruita road), and in the lower part of the Moenkopi formation in the Brush Creek basin north of Vernal, Utah (Pl. 79, fig. 1,2). These specimens remain in the field. Similar impressions may be found at many localities in the Little Colorado Valley of Arizona; for example, the one associated with the supposed jaw impression described above (Pl. 78, fig. 2).

Wherever the "swim" tracks occur there are always present a number of important characteristics, physical and anatomical, which appear to be consistent. No shrinkage cracks indicative of subaerial desiccation or salt crystal pseudomorphs or ripple marks occur anywhere on surfaces bearing "swim" tracks. Also, the mudflat surfaces are usually extensive, roughly circular and apparently do not represent localized stream channels. A portion of an extensive surface as cast on the under side of a thin limestone was carefully excavated and pieced together upside down at a locality north of Vernal (Pl. 79, fig. 1,2). As extensive as this area is, not one definitive footprint nor any definitive series of impressions could be recognized, in marked contrast with typical subaerial mudflats bearing footprints. Occasionally, as shown by the surface at Capitol Reef (Pl. 79, fig. 3), a series of "swim" tracks may be recognized, but even here no full impression of a tetrapod foot can be seen. Most of the tracks appear to be made by the tips of clawless digits with only two—probably digits III and IV—impressing, and all tracks appear to have been made in very soft, dense mud of impalpable grain. One

track in the collection of the University of California shows a blunt-ended digit, lacking a claw and yet possessing a definite scale pattern. This may indicate an aquatic reptile of some kind. All "swim" tracks are probably not marks made while swimming; some appear to have been made by walking motions in shallow water. "Swim" tracks occurring in series at Capitol Reef are definitely similar in mode of impression, though probably not of locomotion, to swim marks made by swimming frogs in the muddy bottom of a shallow standing pool of water.

All characteristics of the Triassic "swim" tracks considered, a reasonable interpretation seems to be that they represent tetrapods moving around mostly by swimming in shallow but extensive pools of a floodplain. Paddling limbs had but to graze the dense mud of the bottom to record a swirling "brush" stroke of the longest digits. It is probable that most of the tracks represent stereospondylous labyrinthodonts which are known to have been common in rivers and pools of Moenkopi time—highly specialized, fish-catching types as well as the more generalized capitosaurs. Some of the tracks could conceivably represent purely terrestrial reptiles such as *Chirotherium* but in any case no "swim" track so far discovered shows a definitive footprint which can be treated as a morphologic type. However one cannot expect better detail on a subaqueous mud surface because the differences in specific gravity and of locomotion of tetrapods in and out of water do not result in comparable records. The value of recognizing "swim" tracks in the Moenkopi adds important data to our knowledge of the paleoecology and sedimentation of that time.

Invertebrate Trails
Pl. 80, fig. 4

McKee (1954) adequately reviews the occurrence of invertebrate trails in the Moenkopi but an occurrence of arthropod trails in the lower Moenkopi (Wupatki member of McKee) near Meteor Crater briefly described by McKee is of more than passing interest because somewhat similar trails are known from the Permian Dwyka tillite of South Africa (Abel, 1935, fig. 238), and I have found in the Lower Triassic *Cynognathus* zone (Pl. 80, fig. 4; 15 miles west of Rouxville, O. F. S.) of South Africa a closely similar trail although of a much larger individual than those which made the Moenkopi trails (Pl. 80, fig. 3).

The arthropod trails from the Moenkopi occur in the same general area and at about the same stratigraphic level (Wupatki member) as numerous labyrinthodont remains and reptilian trackways, but they are not associated on the same surface. The arthropod trail from the *Cynognathus* zone also occurred in the vicinity of and at the same general level as a bonebed containing many therapsid reptiles.

DISTRIBUTION OF VERTEBRATE TRACKWAYS IN THE MOENKOPI FORMATION

Until McKee's excellent study of the regional correlation of the Moenkopi formation from the point of view of lithofacies, the physical evidence was lacking to demonstrate whether the relatively thin type section of the Little Colorado Valley was to be correlated with all or only with some small part of the thick western section. Peabody (1948) had demonstrated that the pseudosuchian trackways of the upper Moenkopi of Utah were more like those of the lower beds of the thin eastern section in Arizona, but hesitated to make formal correlations.

Since 1948, two important facts of distribution of vertebrate trackways in the Moenkopi have become increasingly apparent: first, the trackways in western areas of the Moenkopi (southern and central Utah) occur with one possible exception (Paria lacertoid tracks) in the upper beds, that is, in the upper red member (of H. E. Gregory, 1948); second, the chirotheriid and rotodactylid trackways in Utah are closely related to species occurring in the lower Moenkopi beds (Wupatki member of McKee, 1954) in the Little Colorado Valley of Arizona. *Rotodactylus mckeei* from near Hurricane, Utah, and the undescribed species from Capitol Reef are clearly more primitive, along with *R. cursorius* from the Wupatki member near Meteor Crater, Arizona, than *R. bradyi* from the upper part of the Moenkopi (Holbrook member) near Cameron. The latter species represents a pseudo-

suchian twice as large as the other species and with a definitely shortened pes digit IV —a specialized characteristic of evolutionary significance. Also, all unquestioned chirotheriid footprints so far discovered in Utah are of a giant species most closely related to *Chirotherium moquiense* from the Wupatki member near Winslow and from Wupatki National Monument. *C. barthi*, the most common species in the Holbrook member near Cameron has not been definitely identified in the older Wupatki member and is not yet known from Utah.

McKee (1954) demonstrates on purely physical grounds that the relatively thin section of the type Moenkopi in the Little Colorado Valley is represented only by the upper beds of the much thicker section in southern and central Utah (upper red member and part of the underlying Schnabkaib member). McKee finds that a characteristic massive sandstone prominent in the lower Moenkopi beds of the Little Colorado Valley appears progressively higher in the section from southeast to northwest into Utah. Since the pseudosuchian trackways involved agree in their distribution with the physical facts, and since these trackways are highly characteristic in mode of locomotion and in pedal characteristics, they appear to have definite value as guide fossils within the Moenkopi formation, even in intercontinental correlation (Peabody, 1955).

The length of time represented by the type Moenkopi of Arizona cannot be determined absolutely, of course, but the type section seems to represent something less than half of total Moenkopi time as represented by the Utah section. S. P. Welles (personal communication) believes that the progressive evolution of the otic notch of stereospondylous amphibians found in the Wupatki and Holbrook members of the type Moenkopi indicates a relatively long time span—greater than allowable under McKee's interpretation. Chirotheriid trackways from lower and upper beds of the type section show little temporal evidence of evolution from a quadrupedal to a bipedal gait. However, some progressive evolution of the feet is shown by the rotodactylid species from the Holbrook member, *Rotodactylus bradyi*, in which pes digit IV is shorter than in the older species *R. cursorius*, and by the chirotheriid species from the Holbrook member, *Chirotherium marshalli*, in which the heel carried more body weight than in the older related species, *C. coltoni*. At the present stage of knowledge, evidence of vertebrate trackways, if not of osseous remains, tends to support McKee's conclusions based on physical evidence that the type Moenkopi represents only a late part of total Moenkopi time.

Bock (1952) and especially Baird (1954) describe chirotheriids from the Newark Upper Triassic which illustrate some terminal stages and trends in chirotheriid evolution. On a comparative basis, it appears that the age of the chirotheriid fauna of the type Moenkopi is relatively late rather than early Lower Triassic, and probably is in part, at least, Middle Triassic.

References

Abel, Othenio, 1935, Vorzeitliche Lebensspuren: G. Fischer, Jena, xvi+644 p., 530 fig.

Baird, Donald, 1954, *Chirotherium lulli*, a pseudosuchian reptile from New Jersey: Mus. Comp. Zool. Harvard, Bull., no. 111, p. 165–192, 3 fig., 2 pl.

Bock, Wilhelm, 1952, Triassic reptilian tracks and trends of locomotive evolution: Jour. Paleont., vol. 26, p. 395–433, 4 fig., 10 pl.

Branson, E. B., 1946, Footprints in the Red Peak formation of Wyoming: Geol. Soc. Am., Bull., vol. 57, p. 1181.

Gregory, H. E., 1948, Geology and geography of central Kane County, Utah: Geol. Soc. Am., Bull., vol. 59, p. 211–247, 1 fig., 9 pl.

Gregory, W. K., 1952, Evolution emerging: vol. 2, The Macmillan Co., New York, vii +1013 p., illustr.

Kuhn, Oskar, 1938, Eine Plateosauriden Fahrte aus dem Keuper: Palaeont. Zeitschr., vol. 19, p. 315–321, 5 fig.

Lilienstern, H. R. von, 1938, Fahrten aus dem Blasensandstein des mittleren Keupers von Sudthuringen: Neues Jahrb. Min. Geol. Paläont. (B), vol. 80, p. 63–71, 1 fig., 2 pl.

——, 1939, Fahrten und Spuren im *Chirotherium* sandstein von Sudthuringen: Fortschr. Geol. Paläont., vol. 12, p. 293–387, 28 fig., 12 pl.

Longwell, C. R., 1928, Geology of the Muddy Mountains, Nevada: U. S. Geol. Survey Bull. 798, p. 1–150, 9 fig., 17 pl.

Lull, R. S., 1942, Chugwater footprints from Wyoming: Am. Jour. Sci., vol. 240, p. 500–504, 3 fig., 1 pl.

McKee, E. D., 1954, Stratigraphy and history of the Moenkopi formation of Triassic age: Geol. Soc. Am., Mem. 61, vii+133 p., 19 fig., 12 pl.

Olson, E. C., & Beerbower, J. R., 1953, The

San Angelo formation, Permian of Texas, and its vertebrates: Jour. Geol., vol. 61, p. 389–423, 10 fig.

PEABODY, F. E., 1947, Current crescents in the Triassic Moenkopi formation: Jour. Sedimentary Petrol., vol. 17, p. 73–76, 4 fig.

——, 1948, Reptile and amphibian trackways from the Lower Triassic Moenkopi formation of Arizona and Utah: Univ. California Pub., Dept. Geol. Sci. Bull., vol. 27, p. 295–468, 40 fig., 23 pl.

——, 1955, Occurrence of *Chirotherium* in South America: Geol. Soc. Am., Bull., vol. 66, p. 239–240.

POBORSKI, STANISLAW, 1954, Virgin formation (Triassic) of the St. George, Utah, area: Geol. Soc. Am., Bull. vol. 65, p. 971–1006, 4 fig.

ROMER, A. S., 1945, Vertebrate paleontology: Univ. Chicago Press, ix+687 p., 377 fig.

SCOTT, W. F., 1950, Triassic stratigraphy in the central Wasatch Mountains, Utah: Geol. Soc. Am. Bull., vol. 61, p. 1530.

WELLES, S. P., 1947, Vertebrates from the Upper Moenkopi formation of Northern Arizona: Univ. Calif. Pub., Dept. Geol. Sci. Bull., vol. 27, p. 241–289, 38 fig., 2 pl.

MANUSCRIPT RECEIVED JULY 12, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 741–746, PL. 81, 2 TEXT-FIG., MAY 1956

A NEW ECHINOID FROM THE UPPER DEVONIAN OF ALBERTA

COLIN W. STEARN
McGill University, Montreal

ABSTRACT—A specimen of an echinoid from the upper part of the Fairholme formation is described as *Albertechinus montanus*, n. gen., n. sp. It has narrow, biserial, ambulacral plates with large, subrectangular pores that open into a canal beneath the perradial suture. The interambulacral plates appear to be arranged without order and many show large, primary tubercles surrounded by a ring of scrobicular tubercles.

INTRODUCTION

DURING the summer of 1954 the writer collected a specimen of an echinoid from the Upper Devonian rocks of the Canadian Rockies. As well preserved echinoids are rare fossils in Paleozoic rocks, and the specimen represents a new generic type, a detailed description of it is warranted.

The test was found in the upper part of the Fairholme formation. As the ecological requirements of Paleozoic echinoids are of interest, a description of the geologic setting of the outcrop does not appear to be out of place here. The type locality is on the south side of the North Fork of Hummingbird Creek where it cuts the second range of the Rocky Mountains (Sec. 4, Twp. 36, Rge. 16, W. 5th Mer.) about 820 feet above the base of the Fairholme formation. The locality is about 135 miles northwest of Calgary, Alberta. The Upper Devonian rocks of the Canadian Rockies may be divided into a reef sequence represented by the Fairholme formation and an off-reef or basinal sequence represented by the Flume, Perdrix and Mount Hawk formations (deWitt & McLaren 1950; McLaren 1953). These two facies grade abruptly into one another along the boundary of an ancient barrier reef which passes through the valley of the North Fork of Hummingbird Creek. On the south side of the pass the Fairholme reef sequence is exposed and on the north side the basinal sequence is exposed. The echinoid was found in the argillaceous nodular limestone that overlies the reef wall in the Fairholme formation. The argillaceous limestones are a tongue of the Mount Hawk formation into the dominantly dolomitic Fairholme sequence. They contain a rich fauna of brachiopods and corals some of which are listed below:

Thamnopora cf. *T. cervicornis* de Blainville
Thamnopora cf. *T. polyforata* Schlotheim
Disphyllum colemanense (Warren)
Metriophyllum sp.
Devonoproductus walcotti (Fenton and Fenton)
Schizophoria cf. *S. iowaensis* (Hall)
Atrypa spp.

The habitat of Paleozoic echinoids has been described by Mortenson (1935, p. 49) and Hawkins & Hampton (1927) as lagoonal. The specimen which is the subject of this paper was found in beds overlying a barrier reef but not in the back-reef facies. During the deposition of the argillaceous limestone the area probably stood as a bank slightly higher than the basin to the north but there is no evidence that the limestones were deposited in a protected lagoon.

Due to an unfortunate oversight the specimen was not identified as an echinoid at the time of its collection and therefore no further search was made at the type locality for other specimens. The North Fork of Hummingbird Creek is accessible only by two days travel by horse or on foot from the nearest forestry road. For this reason another opportunity for the collection of additional specimens may not occur for some time.

SYSTEMATIC DESCRIPTIONS

Order LEPIDOCENTROIDA Mortensen
Family LEPIDOCENTRIDAE Loven
Genus ALBERTECHINUS, n. gen.

Description.—Lepidocentridae with narrow, biserial ambulacral areas composed of

many low, transverse, simple ambulacral plates each pierced by two pores elongated in the axis of the plate, and having an inward projection on the perradial end which encloses the radial water vessel and through which the pores pass. Interambulacral plates large, arranged in about 12 rows or without obvious arrangement, the larger ones only containing a large, primary tubercle surrounded by a ring of scrobicular tubercles and with scattered secondary tubercles. Apical and adoral systems unknown.

Genotype.—Albertechinus montanus, n. sp.

Only other known species.—Albertechinus thomasi (Stainbrook). A species which is very closely related to the Alberta one was described by Stainbrook (1937) as *Devonocidaris thomasi*. These two species appear to be cogeneric but neither is a *Devonocidaris* and both are placed in the new genus *Albertechinus*. *Devonocidaris* was founded by Thomas (1920) on isolated plates and spines which taken together give a fairly complete picture of the corona of an echinoid. The characters in which this genus differs from *Albertechinus* may be summarized as follows:

1. The interambulacral plates are thin,
2. There is no scrobicular circlet of tubercles,
3. The pore pairs are not set with their axes parallel to that of the plate,
4. The pores pass directly through the plate,
5. The ambulacral areas are, in part at least, biserial and incorporate hemiplates.

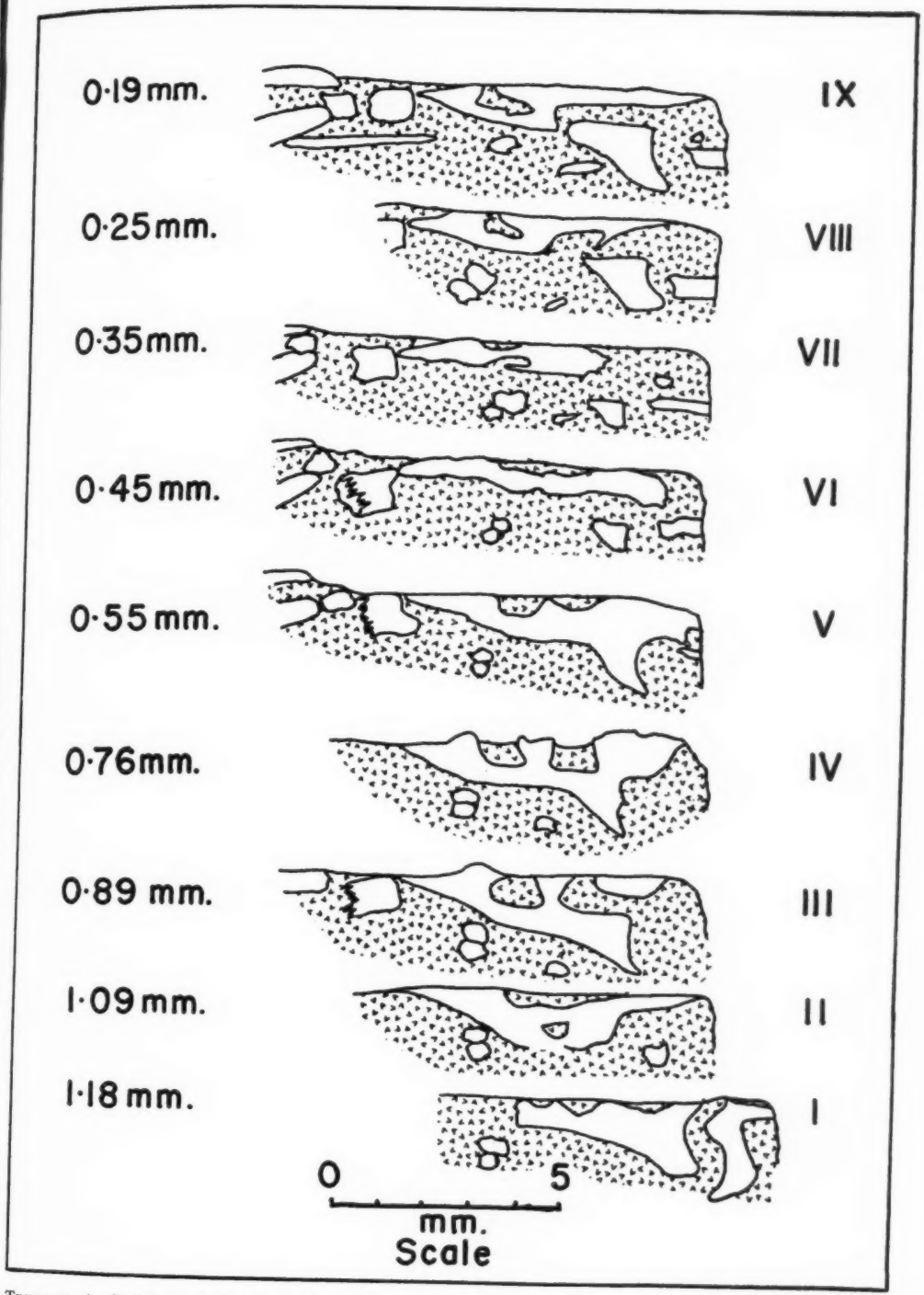
Albertechinus montanus differs from *A. thomasi* in the larger size of its primary tubercles, the greater number of scrobicular tubercles around the primary tubercles (16 to 13), the subrectangular shape of its ambulacral pores, and perhaps in the irregularity of its interambulacral plates.

Discussion.—The classification of Mortensen is adopted in this discussion. The imbrication of the plates of *Albertechinus* and the simplicity of the spines places it immediately in the family Lepidocentridae of the order Lepidocentroida.

Only a few of the Lepidocentridae have interambulacral plates placed apparently without order. For this reason a special effort was made to seek some order out of the plates of *Albertechinus montanus* but only the rudest order is apparent near the adambulacral suture. Collapse of the test on the death of the animal may have caused a jumbling of the plates or they may have been irregular in life. As *Albertechinus thomasi* has well-ordered plates, perhaps this character extends to other species of the genus and will be found in other specimens of *A. montanus*. Some genera characterized by irregular interambulacra are: *Aulechinus*, *Palaeodiscus*, *Echinocystis*, and *Ectinechinus*. In *Palaeodiscus* and *Echinocystis* systematic arrangement of the plates has been seen in some specimens and this has prompted Mortensen to write (1935, p. 65) " . . . it is scarcely possible to draw a definite line of distinction between the irregular and regular columnar arrangement." If *A. montanus* is proved to have irregular interambulacra, it will be exceptional, for all other Devonian echinoids have progressed beyond this stage to an orderly arrangement.

By Devonian time the Lepidocentridae were well along the way to specializing their ambulacral systems by multiplying the number of rows of tube feet. The start of this tendency may be observed as early as Silurian time in *Echinocystis* and culminates in such genera of the late Palaeozoic as *Lepidesthes*. It appears that *Albertechinus* has been left out of this evolutionary trend for even at the ambitus there is no suggestion of the occlusion of plates. *Nortonechinus* has similar ambulacral plates but differs in the regularity of its interambulacral plates and the structure of its pores.

One of the most interesting primitive features of this genus is the presence of a cavity beneath the perradial suture into which the pores open. Such a cavity has been described fully in *Aulechinus* and *Ectinechinus* by MacBride & Spencer (1939), has been suspected in *Palaeodiscus* (Mortensen, 1935, p. 55), appears in modified form in *Koninckocidaris*, and is reduced to a channel bordered by spiniform processes in *Hyattechinus* and *Lepidechinoides* (Cooper, 1931). The processes bordering the cavity are suggested in the descriptions of Thomas (1920) and Belanski (1928) of *Nortonechinus*. Reconstructed sections through the ambulacral plates of some of the Lepidocentridae are shown in Text-figure 2 for comparison with that of *Albertechinus*. The new genus falls midway between *Aulechinus* of the Ordovician and *Meekechinus* of the Permian in the evolutionary series showing the reduction of these perradial processes.



TEXT-FIG. *1*—Serial sections of a half of the ambulacral and a small part of the interambulacral area of *Albertechinus montanus*. The perradial suture is on the right side of the diagram and the adradial suture near the left side. The measurements on the left indicate the distance of the sections from the plane of the thin section that was the final product of the grinding. Matrix in checked pattern; plates clear.

The ambulacral plates differ from those of most other genera in having large elongate pores. In a general way the plates resemble those of *Lepidocentrus* but the pores are not round and simple. The size of the pores and the horizontality of their axis is enough to distinguish them from any other genus.

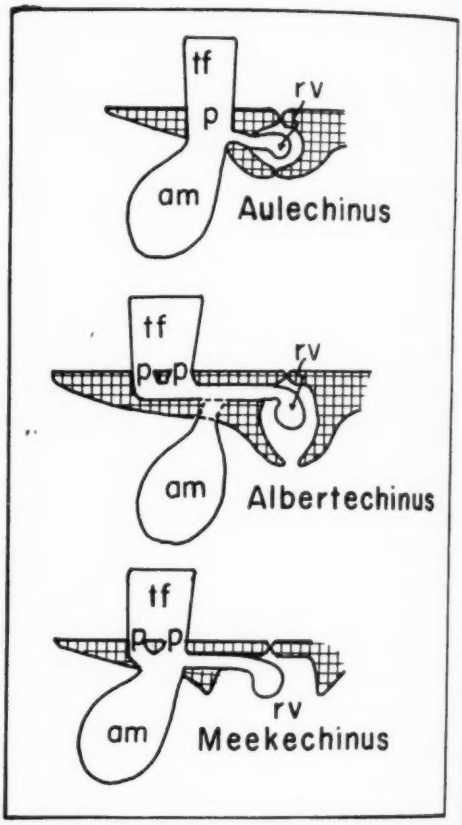
The large primary tubercle on many of the interambulacral plates is similar to that found in the genera *Nortonechinus*, *Lepidocentrus*, and *Perischodomus*. In the first of these genera each plate carries a tubercle but these are much like those of *Albertechinus*. In *Lepidocentrus* the tubercles are much smaller and scarcely larger than the secondary ones. *Perischodomus* may be easily distinguished from *Albertechinus* by its several rows of ambulacral plates.

ALBERTECHINUS MONTANUS, n. sp.
Pl. 81, fig. 1–3; Text-fig. 1

Description of specimen.—The specimen is discoidal and measures 6 cm. in diameter and 2 cm. in maximum thickness. The plates of the echinoid that are systematically arranged are confined to one flat face and the reverse face shows only scattered plates and a few small spines. The reverse face is described in more detail below. The specimen shows clearly about one eighth of the test of the echinoid and includes the apical part of three interambulacral areas, the apical half of one ambulacral area, and a small part of another ambulacral area. Neither the apical system, periproct, peristome, or lantern is preserved. Ventrally the specimen ends near the ambitus, dorsally, a few plates below the apical system. The convergence of the two ambulacral areas to within a few plates of each other at the top of the specimen indicates that only a few plates below the periproct are missing.

Original size and shape of test.—In many specimens of Paleozoic echinoids the two sides of the corona are crushed back to back during preservation. Sectioning shows that this is not the manner of preservation in the specimen under discussion. The space behind the wall of plates is occupied by loose, scattered plates and spines and no opposite wall can be recognized. Little, then, can be said about the shape of the test in life. The low curvature of the coronal plates of the specimen in both the equatorial and verticle planes suggests that the animal was spherical and fairly rigid during life despite the flexibility given by the imbricating plates. If this is true, then rough estimates may be made for the total size of the corona from the fragment: the total height was probably between 12 and 15 cm. and the diameter about 10 cm.

Ambulacral areas.—Only one ambulacral area is satisfactorily exposed and most of the following description is based on it. The area is narrow compared with the interambulacral area, only 9.1 mm. in maximum width. The ambulacral plates bevel conspicuously under the adambulacral plates. This beveling, which has undoubtedly been



TEXT-FIG. 2—Diagramatic cross sections of the ambulacral plates of some Paleozoic echinoids showing the relationship of the pores to the water vascular system. *Aulechinus* (Ordovician) after MacBride & Spencer, *Meekechinus* (Permian) after Moore, Lalicker and Fischer. tf—tube foot, p—pore, rv—radial water vessel, am—ampulla.

emphasized by movement of the plates after death, causes the area to appear as a trench. A cross profile of this ambulacral trench would show it to be arched in the center and marked axially by the small groove of the perradial suture. The area narrows slightly adapically but is of constant width along most of its preserved length. The ambulacral plates are biserial, narrow, and numerous. Fourteen occupy the space of 10 mm. and 8 to 10 of them occupy the space opposite one adambulacral plate. The plates like those of most of the Lepidocentridae imbricate adorally but this is not obvious in casual examination and the amount of imbrication is small. A large part of each plate is occupied by two simple, large, pores which are surrounded by a slightly sunken area. This area is bounded adorally by a small ridge on the edge of the plate. The pores are oval or almost subrectangular in plan. The long sides are almost straight and parallel to the margins of the plate but the ends of the pores are rounded. The outside pore tends to be slightly larger than the inside pore but this is not universally true. The pores are about 0.5 mm. long and about 0.3 mm. wide. The plates are rather badly weathered so that few surface characters can be distinguished. However, they appear to thicken on either side of the pore-pair and this thickening may mark the location of a tubercle for the attachment of a spine. The plates are not quite rectangular but curve adapically where they meet in the zigzag perradial suture.

The internal structure of the ambulacral plates of the Lepidocentridae has been the subject of considerable discussion. As the inside of the test is filled with matrix, this information can only be gained from this specimen from serial and thin sections. A small fragment was cut from the end of the ambulacral area and cemented to a glass slide. This fragment was ground down on a carborundum plate and during this grinding the specimen was examined under the microscope and drawings were made at intervals measured by a micrometer. Text-fig. 1 represents these drawings and the following discussion is based on this figure. The imbrication of the plates cannot be detected in these sections but two of the sections (II and VII) pass close to the boundary between plates. Except near its edges, the ambulacral plate is wedge-shaped in cross-section with its thickest part along the perradial suture. The two pores are shown in sections III, IV, V, and IX. The connection of the outside pore to any other cavity cannot be demonstrated in the sections but the pore is believed to pass laterally into the inside pore between the sections. Section VII suggests that this pore is connected directly to the interior of the test near the edge of the plate but this effect is caused by an irregularity in the lower surface of the plate. The inside pore passed by a wide canal into a cavity inclosed within the two ambulacral plates, a cavity which presumably housed the radial water vessel (sections III, IV, and IX). This cavity can be seen in entirety only in section I where the inside edge of the other ambulacral plate is preserved but has slipped slightly out of position. The inner pore communicates with the inside of the test not directly but by a canal joined to the lateral canal to the radial water vessel (VII, IX). In sections IV and III protuberances appear on the top of a plate that may be tubercles for spines. The adradial suture is not at all clear in these sections although it is certain that the interambulacral plates overlap on the ambulacral plates. In all sections the thin outer edge of the ambulacral plate is in contact with a subrounded calcareous plate that may be the broken end of an interambulacral plate. The area beneath the ambulacral area is filled with disordered, broken plates and spherical bodies of calcite set in a fine grained calcite matrix. The thin section shows that all the plates are single calcite crystals and exhibit the calcite cleavage throughout.

Interambulacral areas.—The interambulacral area is wide compared with the ambulacral area but its complete width is not exposed near the ambitus. It appears to have been about 3.5 cm. across. The plates are arranged in no definite rows or zones except near the ambulacral suture. The ambulacral areas are bordered by rows of regular adambulacral plates but apart from these rows there is little order either as to size or position of the plates in the interambulacral area. The plates imbricate adorally and towards the ambulacral areas. The center of the interambulacral area was occupied by a row of small plates that lie on top of their neighbours on either side. These

can be distinguished only near the top of the specimen. The interambulacral plates are relatively large and subrounded in shape but their true dimensions are hidden by their imbrication. The largest measures 8.7 mm. in vertical dimension and 5.9 mm. in lateral dimension. The thin section shows that these plates are about 1 mm. thick. Many, but not all of the interambulacral plates have a large, central, primary tubercle surrounded by an aureole and a ring of scrobicular tubercles about 16 in number. The primary tubercles are well preserved and regularly developed on all the adambulacral plates and on the larger of the other plates. Secondary tubercles are irregularly scattered on the smaller interambulacral plates and around the primary tubercles on the larger plates. The tubercles are not perforated but this may be owing to the type of preservation. The thin section shows that the surface of some of the plates was covered with tiny pits that are now filled with matrix.

Spines.—No primary spines have been found associated with this specimen. Secondary spines intersected in the thin section are deeply striated longitudinally and have a simple internal structure. In these features they are similar to the described lepidocentrid and modern echinothurid spines.

Reverse side of specimen.—On the reverse side of the specimen the plates are scattered and few in number. Most of them are large, subhexagonal, interambulacral plates showing a primary tubercle. A few are ambulacral plates with their large double pore. Those that lie on their sides confirm the evidence of the serial sections as to the projection of the plate inward at the perradial suture.

Repository.—The specimen has been deposited in the holotype collection of the Geological Survey of Canada at Ottawa where it is No. 12,770.

Associated Echinoid Remains

The argillaceous limestone unit of the upper Fairholme formation and the equivalent part of the Mount Hawk formation also contain scattered spines and plates of doubtful affinities. Some of these are expanded greatly at their distal ends to form a round, thick, plate. Their proximal ends are narrow, straight, and have a small depression (acetabulum). There is no milled ring (Pl. 81, fig. 4). Spines similar to these have been described as *Nortonechinus* by Thomas (1920). They are tentatively referred to that genus here but may belong to *Albertechinus* although they have not been found associated with the test.

ACKNOWLEDGMENTS

The writer is grateful to the Canadian Gulf Oil Company for the opportunity to collect and study the specimen here described. This paper is published with the kind permission of Canadian Gulf Oil Company, Calgary, Alberta.

REFERENCES

BELANSKI, C. H., 1928, Description of some typical fossils of the Shellrock stage: Am. Midland Naturalist, vol. 11, p. 181.

COOPER, G. A., 1931, *Lepidechinoides* Olsson, a genus of Devonian echinoids: Jour. Paleont., vol. 5, p. 127–142.

DEWIT, R., & MCLAREN, D. J., 1950, Devonian sections in the Rocky Mountains between Crowsnest Pass and Jasper, Alberta: Canada Geol. Survey Paper 50-23.

HAWKINS, H. L., & HAMPTON, S. M., 1927, The occurrence, structure, and affinities of *Echinocystis* and *Palaeodiscus:* Geol. Soc. London Quart. Jour., vol. 83, p. 574–603.

MACBRIDE, E. W., & SPENCER, W. K., 1939, Two new Echinoids, *Aulechinus* and *Ectinechinus* and an adult plated holothurian from the Upper Ordovician of Girvan, Scotland: Royal Soc. London Philos. Trans., ser. B, vol. 229, p. 91–136.

MCLAREN, D. J., 1953, Reef development in the Devonian of the Canadian Rocky Mountains: Canadian Min. Met. Bull., vol. 46, p. 706–710.

MORTENSEN, TH., 1935, A monograph of the Echinoidea, vol. 2, Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta: Reitzel, Copenhagen and Milford, Oxford, New York.

STAINBROOK, M. A., 1937, New echinoderms from the Devonian Cedar Valley formation of Iowa: Am. Midland Naturalist, vol. 18, p. 899–904.

THOMAS, A. C., 1920, Echinoderms of the Iowa Devonian: Iowa Geol. Survey, vol. 29, p. 500.

MANUSCRIPT RECEIVED SEPTEMBER 30, 1955

EXPLANATION OF PLATE 81

FIG. *1–3—Albertechinus montanus*, n. sp. Holotype, GSC 12770. *1*, ×1. *2*, interambulacral plates, ×6. *3*, ambulacral plates and adambulacral plates showing primary tubercles, ×6.

4—?Nortonechinus sp. GSC 12771, ×2.2; from Fairholme formation, first creek south of Cripple Pass, Ram Range, Alta.

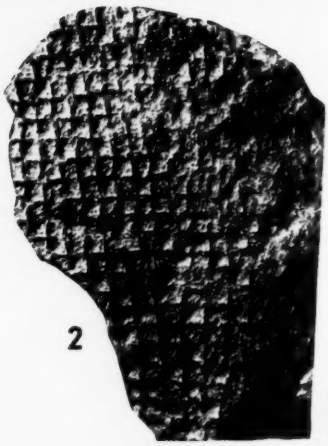
1

2

3

4

1



2

3

4

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 747–759, PL. 82, 6 TEXT-FIG., MAY 1956

PALEONTOLOGICAL NOTES

RECEPTACULITES IN THE UPPER DEVONIAN OF NEW YORK

JOHN W. WELLS
Cornell University

ABSTRACT—The occurrence of *Receptaculites* in the Upper Devonian of New York is recorded for the first time. The specimen is placed in affinity with *R. monticulatus* Hall, from the earlier Devonian of New York, and is remarkably like the type species, *R. neptuni*, from the Frasnian of Europe.

The problematical sponge-like fossil *Receptaculites*[1] has not been reported from the Upper Devonian of New York, although it occurs in older strata in this state and adjacent areas. It is therefore of interest to record the discovery of the remains of a large specimen in the lowest part of the Upper Devonian in the Finger Lakes region.

The specimen was found last year by Mrs. Herbert W. Briggs of Ithaca, New York, on a slab of shaly siltstone she had selected for use on a terrace paving. The writer is happy to acknowledge here his thanks to her for her recognition of a significant fossil and for presenting it to the Paleontological Laboratory at Cornell. The slab was found by Mrs. Briggs loose in the bed of Monkey Run, a small tributary of Fall Creek, 3.25 miles northeast of the Cornell campus (Ithaca East, 1:24,000 sheet). The stratigraphic horizon at this spot would be in the lower part of the Enfield formation (Senecan series), if there were any outcrop. The well-worn condition of the slab and lack of bedrock outcrop indicates strong possibility of glacial transport from some horizon to the north. No such lithology occurs in the Middle Devonian rocks in this region, but some 600 feet of non-calcareous shales, siltstones, and flags intervene between the top of the Middle Devonian (Geneseo black shale) and the Enfield. In addition to *Receptaculites* the slab shows on its surface many fragments of colonies of *Cladochonus*, a tabulate coral characteristic of two local horizons, one at the base of the Sherburne formation overlying the Geneseo, and the

[1] De Laubenfels (1955, p. 108) has indicated that *Receptaculites* de Blainville, 1830, is a junior synonym of *Receptacule* Defrance, 1827, and that he is retaining de Blainville's name (ICZN decision pending), so long in use, but he has apparently overlooked an earlier junior synonym, *Receptaculites* Deshayes, 1828. Deshayes attributes the name to Defrance, and it is quite possible that both he and de Blainville recognized the original spelling as a lapsus calami.

EXPLANATION OF PLATE 82

Receptaculites in the Upper Devonian of New York, by John W. Wells.

FIG. *1,2*—*Receptaculites* sp. aff. *R. monticulatus* Hall, basal Sherburne (lowest Senecan), Monkey Run, Tompkins Co., N. Y. (Cornell Univ. Paleont. Coll. No. 40021). *1*, general aspect, ×0.5; *2*, natural mold of exterior surface, ×1. (p. 747)

The ammonoids *Koenenites* and *Beloceras* in the Upper Devonian of New York, by John W. Wells.

FIG. *3*—*Koenenites cooperi* Miller, Lower West River shale (lower Senecan), Canandaigua Lake, Ontario Co., N. Y. (Cornell Univ. Paleont. Coll. No. 40022): mold of last few chambers and living chamber, ×4. (p. 749)

4—*Beloceras williamsi*, n. sp., lower Cayuta shale (upper Senecan), Bald Hill, Tompkins Co., N. Y. (Cornell Univ. Paleont. Coll. No. 40023): holotype, ×1. (p. 751)

Partial cost of the plate defrayed by the W. L. E. Gurley Foundation for Paleontology of Cornell University.

other in the upper part of the Sherburne. Splitting the slab in the laboratory to reduce its bulk fortunately revealed a conch of the ammonoid *Ponticeras perlatum* (Hall), which occurs in particular abundance in the basal Sherburne *Cladochonus* zone in the Cayuga Lake region and scatteringly up to the lower part of the overlying Ithaca formation. The writer believes the slab originated in the basal zone.

The *Receptaculites* is represented by the mold of part of the outer surface of a large, partly macerated individual that is now flattened by compression and compaction (Pl. 82, fig. 1). The maximum expanse preserved is 28 centimeters. There is no indication of the basal point around which the outer pavement of rhombic plates, 4–5 mm. in size, was quincunxially centered, and the fragment is probably only part of a very large specimen as much as 50 centimeters across. There is no trace of the vertical rays, the summit plates are indicated only in vague outline, but the impressions of the four horizontal rays radiating from the vertical rays just underneath the summits' rhombs are well defined (Pl. 82, fig. 2). The lozenge shape of the summit plates and the horizontal ray impressions are characteristic of both *Receptaculites* and the very closely related *Ischadites*. The latter differs from *Receptaculites* by its longer vertical rays, greater wall thickness, lack of an inner "wall," and smaller central cavity (Rauff, 1892). Both general range from the Ordovician into the Devonian, and the present specimen, lacking as it does any details of the inner structures, could pertain to either genus, although it is much larger than is usual in *Ischadites*.

Both *Receptaculites* and *Ischadites* are known from the Helderbergian (Lower Devonian) of New York: *R. infundibuliformis* (Eaton) (=*R. monticulatus* Hall[2]) and *I. squamifer* Hall, both from the New Scotland formation. *R. bursiformis* Hall occurs in the Schoharie formation (Ulsterian). *R. monticulatus* and *R. bursiformis* are probably the same species, and superficially are certainly very much like the Monkey Run specimen (cf. Hall & Simpson, pl. 24, fig. 10 and 12). The rhombic summit plates are smaller in *R. monticulatus* (1 to 4 mm.) and *R. bursiformis* (2.5 mm.).

It is obviously impracticable to designate the Upper Devonian specimen as a new species on the basis of such a slender difference as somewhat larger summit plates, and it is here merely affiliated with the older forms as *R.* sp. aff. *R. monticulatus* Hall. It could just as well be referred to *R. neptuni*, the type of the genus, originally described from horizons corresponding to the Senecan (Frasnian) in Belgium, subsequently found in the Upper Devonian elsewhere in Europe, and erroneously identified from the Ordovician on North America. According to Waterlot, in his careful analysis of the Belgian material (1932), the external rhombs or lozenges of *R. neptuni* measure 5 mm. on the short diagonal and 7 mm. on the long. The Monkey Run specimen is very closely allied to its Hercynian contemporary.

[2] *Coscinopora infundibuliformis* Eaton 1832, *non C. infundibuliformis* Goldfuss 1826, which is a European Cretaceous sponge.

REFERENCES

De Laubenfels, M. W., 1955, Porifera, in: Treatise on Invertebrate Paleontology, Part E, p. 21–122.

Deshayes, G. P., 1828, Réceptaculite: Dictionnaire Classique d'Histoire Naturelle (ed. Bory de Saint-Vincent), t. 14, p. 486.

Hall, J., & Simpson, G. B., 1887, Palaeontology of New York, vol. 6 (Corals and Bryozoa): iv+298 p., 66 pl.

Rauff, H., 1892, Untersuchungen über die Organisation und systematische Stellung der Receptaculitiden: K. bayerische Akad. Wissen., M.-P.Cl,. Abh., Bd. 17, p. 645–722, 11 fig., pl. 1–7.

Waterlot, G., 1932, Structure et position systématique du *Receptaculites neptuni* Defrance: Soc. Géol. Nord, Ann., t. 57, p. 2–12, 10 fig., 2 pl.

Manuscript received December 7, 1955

THE AMMONOIDS *KOENENITES* AND *BELOCERAS* IN THE UPPER DEVONIAN OF NEW YORK

JOHN W. WELLS
Cornell University

ABSTRACT—Specimens of the ammonoids *Koenenites cooperi* Miller from the West River shale (Genesee group) and *Beloceras williamsi*, n. sp., from the lower Cayuta shale (Chemung group) of central New York are described. *Koenenites* was previously known only from Michigan and Europe; *Beloceras* is reported for the first time in North America. Both genera occur at horizons low in the Upper Devonian of New York, paralleling their occurrence elsewhere.

Slowly the Upper Devonian deposits of New York are yielding fossils which contribute further to the precise correlation of these beds. Recent discoveries are of representatives of the ammonoids *Koenenites* and *Beloceras* at horizons where they would be expected to occur if current correlations are correct. Notes on these occurrences follow.

Genus KOENENITES

Last summer the writer spent some time cruising along the west shore of Canandaigua Lake, New York, searching for cephalopods in the Upper Devonian West River shale. As so often happens in such purposeful searchings only a few miserable fragments were found. Fortunately they were not thrown away, for one proved to retain a few sutures whose pattern fitted none of the New York Devonian ammonoids so carefully monographed by A. K. Miller (1938).

KOENENITES COOPERI Miller

Pl. 82, fig. 3; Text-fig. 1A,1B

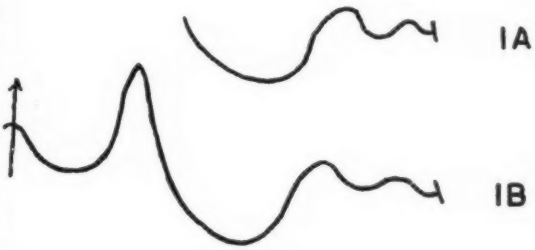
Koenenites cooperi MILLER, 1938. Geol. Soc. Am., Spec. Paper 14, p. 126, pl. 27, fig. 8–11; pl. 28, fig. 1–5; text-fig. 25,26.

The single specimen is an internal mold of part of a small conch retaining part of the outer volution, about 10 mm. in height, with traces of the dorso-lateral part of the last two sutures (Text-fig. 1A), and a faint trace of the inner whorls. The suture shows clearly the additional lateral lobe that distinguishes this genus from *Manticoceras*. Its pattern, as can be seen by comparison with the mature suture of *K. cooperi* (Text-fig. 1B) is almost exactly like that species. The ratio of umbilical radius to conch radius in both is the same, nearly 1:4.

K. cooperi, the only representative of the genus yet known in North America and outside of Europe (Miller, 1938, p. 126), occurs in the base of a limestone just below the Antrim shale in Michigan. This is the Squaw Bay limestone of Warthin & Cooper (1935), which has been correlated with the Genundewa limestone of New York (Cooper et al., 1942, p. 1782). The two formations are regarded by Cooper as the lowest Upper Devonian in the eastern United States on the basis of *Koenenites* in the Squaw Bay. In Europe the genus is confined to the lowest part of the *Manticoceras* zone (Iα). In central New York the West River shale with *Koenenites* immediately overlies the Genundewa. *Koenenites* might be expected to occur in the Genundewa, and the writer has collected one specimen from this limestone which may well be *K. cooperi*. Its proportions are the same as those of *K. cooperi* and quite different from those of *Manticoceras apprimatum*, the common species in the Genundewa, but while the growth lines are beautifully shown, there are no traces of the sutures.

Figured specimen.—Cornell Univ. Paleont. Coll. No. 40022.

Horizon and locality.—Lower West River



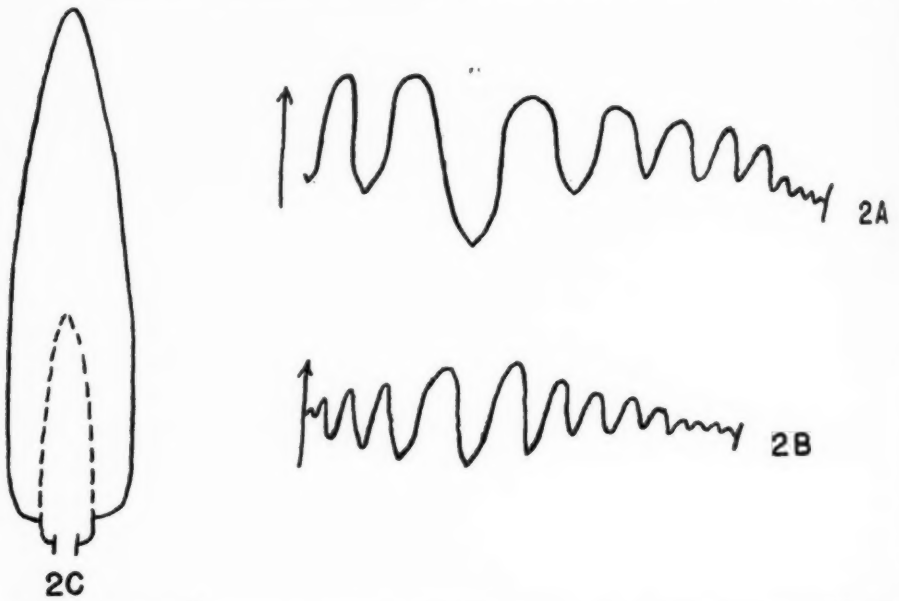
TEXT-FIG. 1—*Koenenites cooperi* Miller: A, external suture of specimen from West River shale, central New York, ×4; B, external suture of typical specimen from Squaw Bay limestone, Michigan, ×3.5 (Miller, 1938, test-fig. 26F).

shales (Genesee group = lower Finger Lakesian stage = lowest Senecan series), west shore of Canadaigua Lake, 0.6 mi. south of Hicks Point, Ontario Co., N. Y.

Genus Beloceras

In western Europe, especially Germany, this genus is characteristic of the upper part of the *Manticoceras* zone (ammonoid zone I = Frasnian). It occurs at the same horizon in Russia and Morocco (Miller 1938, p. 134), as well as in Western Australia (Teichert, 1941, p. 150; 1949, p. 18). *Beloceras* is strikingly different from its contemporary tornoceratids in its discus shape and multilobate sutures which give it an advanced aspect. Relatively easy identification, limited temporal and wide distribution give it a high stratigraphic value. Heretofore it has not been found in North America, and its discovery at the appropriate horizon in the Upper Devonian of New York is therefore highly significant.

This lone American specimen of *Beloceras* was found about six years ago by the writer in a shaly siltstone in the lower part of the Chemung group (upper Senecan series) not far from Ithaca, New York. The associated benthonic brachiopod-pelecypod assemblage is of mingled Tioughniogan (Hamilton) and Chemungian aspect: *Elytha fimbriata* (Conrad), *Spinocyrtia marcyi* (Hall), *Ambocoelia umbonata* (Conrad), *Modiomorpha concentrica* (Conrad), and *Cypricardella bellistriata* (Conrad); *Mucrospirifer mucronatus posterus* (Hall & Clarke), *Schizophoria impressa* Hall, *Cariniferella tioga* (Hall), and *Productella lachrymosa* Hall. In the brachiopod zonation of the Upper Devonian on the Cayuga Lake meridian first set forth by H. S. Williams (1884, 1909, 1913) this horizon is about 150 feet above the *Thiemella* (?) *danbyi* zone (initial appearance of *Cyrtospirifer* [*perlatus*-form]) which lies at the base of the Cayuta shale, and about the same distance below the second *Tropidoleptus* zone in the top of the Cayuta. This is well up in the known range of *Manticoceras* in New York (from middle Finger Lakesian into the Cassadagan). The Chemungian has been correlated with the upper Frasnian of Europe (Cooper, et al., 1942, int. al.), a parallelism now materially strengthened. But if we are to accept the upper boundary of the Frasnian as being the top of the *Manticoceras* zone, the Frasnian-Famennian boundary equivalent in New York should be raised to include the lower



Text-fig. 2—A, external suture of *Beloceras williamsi*, n. sp., ×1, B, external suture of *B. multilobatum*, ×1 (Miller, 1938, text-fig. 28D); C, restored outer whorl section of *B. williamsi*, ×1.

part of the Chautauquan series (Cassadagan stage), as hinted by Miller (1938, p. 9,12) and Schmidt (1949, p. 214).

The New York *Beloceras* represents a new species, here named in honor of Henry Shaler Williams.

BELOCERAS WILLIAMSI, n. sp.
Pl. 82, fig. 4; Text-fig. 2A,2C

Conch large (up to 150 mm. diameter), discoidal and ammoniticonic. Whorls deeply impressed dorsally and gently convex laterally, greatest width about one-third the distance ventrad from the umbilical shoulder. Height of whorl at last suture, 76 mm. Umbilicus relatively small with respect to conch diameter (about 1:7); shoulder rounded with very steep walls. Mature suture as shown in Text-fig. 2A, consisting externally of a total of 11 pointed lobes and rounded saddles, of which the ninth ventrad from the umbilical seam is the largest. The extreme ventral part of conch and suture are not shown on the specimen, but not more than a millimeter or two can be missing.

The holotype, an internal mold (part and counterpart), shows the last seven chambers and several centimeters of the living chamber, and the umbilicus. In general form, relative proportions, and maximum size, this species is very close to the common *B. multilobatum* (von Beyrich) from the *Manticoceras* beds ($I\beta$-δ) in Europe, but it has fewer auxiliary ventral lobes. In both species the ninth lobe ventrad of the umbilical seam is the largest, but in much smaller but adult specimens of *B. multilobatum* there are at least three or four lesser ones between the ninth and the venter (Text-fig. 2B from Miller, 1938), compared with only two in *B. williamsi*.

Holotype.—Cornell Univ. Paleont. Coll. No. 40023.

Horizon and locality.—Lower part of the Cayuta shale member (Chemungian stage, upper Senecan series), about 150 feet above the *Thiemella* (?) *danbyi* zone (=base of Cayuta), on Bald Hill, elev. 1750′, 2 miles southeast of Brooktondale, Tompkins Co., N. Y.

REFERENCES

COOPER, G. A., et al., 1942, Correlation of the Devonian formations of North America: Geol. Soc. Am., Bull., vol. 53, p. 1729–1754, 1 fig., 1 pl.

MILLER, A. K., 1938, Devonian ammonoids of America: Geol. Soc. Am., Spec. Paper 14, 262 p., 39 pl., 41 fig.

SCHMIDT, H., 1949, Ein Vergleich zwischen deutschem und amerikanischem Devon: Deutsche geol. Ges., Zeitschr., Bd. 101, p. 213–219, 1 fig., 1 pl.

TEICHERT, C., 1941, Upper Devonian goniatite succession of Western Australia: Am. Jour. Sci., vol. 239, p. 148–153.

——, 1949, Observations on stratigraphy and paleontology of Devonian: Western portion of Kimberley Division, Western Australia: Bureau of Mineral Res., Geol. and Geophysics, Comm. Australia, Rept. no. 2, 55 p., 1 fig., 2 tables, 6 pl.

WARTHIN, A. S., & COOPER, G. A., 1935, New formation names in the Michigan Devonian: Washington Acad. Sci., Jour., vol. 25, p. 524–526.

WILLIAMS, H. S., 1884, On the fossil faunas of the Upper Devonian along the meridian of 76° 30′ from Tompkins Co., N. Y., to Bradford Co., Pa.: U. S. Geol. Survey, Bull., 3, 36 p.

——, TARR, R. S., & KINDLE, E. M., 1909, Watkins Glen-Catatonk Folio: Geol. Atlas, U. S., 242 p., 6 maps, 37 fig. ("field edition").

——, 1913, Recurrent *Tropidoleptus* zones of the Upper Devonian in New York: U. S. Geol. Survey, Prof. Paper 79, 103 p., 6 pl., 18 fig.

MANUSCRIPT RECEIVED DECEMBER 7, 1955

For explanation of Plate 82, please turn to p. 747.

A NEW BIVALVE GENUS AND SPECIES FROM THE RIPLEY FORMATION OF MISSISSIPPI[1]

LLOYD WILLIAM STEPHENSON
U. S. Geological Survey

ABSTRACT—A new genus and species of bivalve mollusk found in the upper part of the Ripley formation in a cut of State Highway 30, 3.4 miles northeast of New Albany, Union County, Mississippi, is described under the name *Hilgardia compressa* Stephenson in the family Mytilidae. This shell is unusual in that among hundreds of collections no representative of the genus has been found elsewhere in the Upper Cretaceous of the Atlantic and Gulf Coastal Plain.

The shells of the new molluscan bivalve genus and species described in this paper were found by Dr. Norman F. Sohl and me on April 12, 1955 in a cut on State Highway 30 about 3.4 miles northeast of New Albany, Union County, Mississippi (E½ sec. 30, T. 6. S., R. 4. E.). We were at the time engaged in a study of the stratigraphic relationships and the faunal content of the Ripley formation and the overlying Prairie Bluff chalk in northern Mississippi.

This cut together with several other cuts within a quarter of a mile to the southwest afford an almost complete section from the basal part of the Clayton formation (Paleocene), a weathered facies, downward through the Prairie Bluff chalk and through the upper Ripley nearly to its contact with the underlying McNairy sand (=tongue in Mississippi). Sohl measured and described this section and determined the position of the bed containing this new mollusk to be about 105 feet below the contact of the Ripley formation with the overlying Prairie Bluff chalk. In a forthcoming paper he will publish a detailed description of the section and preliminary lists of the fossils collected. The macrofauna associated with this new form includes many species, mainly marine mollusks, but also a few corals, annelids, echinoids, bryozoans, and vertebrates (shark teeth, fish vertebrae and otoliths). Descriptions of the new genus and species are given below. This new form is referred to the family Mytilidae, its closest affinities apparently being with the genus *Modiolus* Lamarck.

[1] Publication authorized by Director, U. S. Geological Survey.

Family MYTILIDAE

Genus HILGARDIA Stephenson, n. gen.

Type species: *Hilgardia compressa* Stephenson.

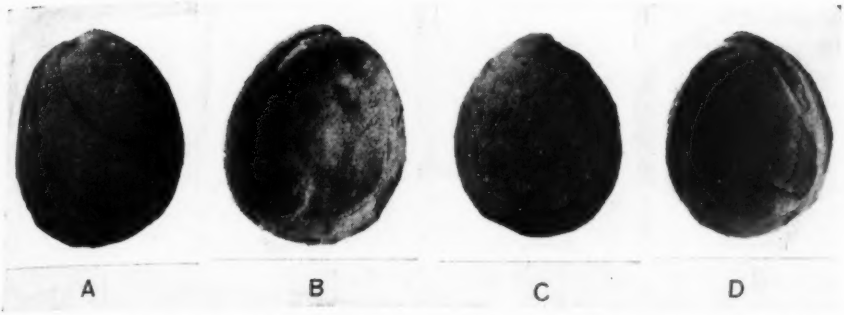
Etymology: Named in honor of the late Eugene W. Hilgard, a distinguished pioneer American Geologist, and onetime State Geologist of Mississippi.

Shell small, compressed, ovate in outline, nearly equilateral, equivalve. A posterior gape if present must be very narrow. Beaks small, nonprominent, prosogyrate, situated centrally. Ligament seated in a deep narrow groove that extends from just below the beak in a broad curve rearward and inward to the inner margin. Hinge edentulus. Anterior adductor scar elongate, situated high in the shell immediately below the dorsal margin just in front of the beak; posterior adductor scar broadly subovate, a little larger than the anterior scar, situated low in the shell near the margin a little back of the center. Pallial line simple and near the margin. Inner surface and inner margin smooth. Outer surface with fine concentric growth lines and rather weakly developed resting stages. The edges of broken shell fragments show an outer thin lamellar, nacreous layer and an inner proportionately very thick prismatic layer.

The genus differs from *Modiolus* Lamarck in its more compressed form, its more broadly ovate outline, and its lack of an anterior wing or ear.

HILGARDIA COMPRESSA Stephenson, n. sp.
Text-fig. 1,A–D

The important characters of this species are described under the generic heading. The



TEXT-FIG. 1—*Hilgardia compressa* Stephenson, n. sp. *A*, *B*, Exterior and interior views of holotype, a left valve, *C*, *D*, Exterior and interior views of a paratype, a right valve. All ×2.

shell is unusual in that, among the hundreds of collections made from Upper Cretaceous beds during past years in the Atlantic and Gulf Coastal Plain, no representatives of this genus have heretofore been recorded.

The dimensions of the holotype, a left valve, are: Length 12.2 mm., height 14.2 mm., convexity 3.9 mm. The largest paratype, a left valve, measures: Length 14 mm., height 15.5 mm., convexity 5 mm.

Types.—Holotype, a left valve, USGS 25485, USNM 125055; one figured paratype, a right valve, from same source, USNM 125056; five unfigured paratypes and several fragments, from same source, USNM. 125057.

Occurrence.—Cut on state Highway 30 about 3.4 miles northeast of New Albany, 1.25 miles southwest of Keownville, in SE¼ sec. 30, T. 6 S., R. 4 E., Union County. Mississippi.

MANUSCRIPT RECEIVED SEPTEMBER 6, 1955

MYTONOMYS, A NEW GENUS OF PARAMYID RODENT FROM THE UPPER EOCENE

ALBERT E. WOOD
Department of Biology, Amherst College

INTRODUCTION

In the course of preparing a monograph of the extinct rodent family Paramyidae, a number of forms have been identified which must be considered to be new genera. Most of these will be described in the monograph in question. But Dr. Loris S. Russell has asked me to publish on one of them, since he wishes to describe additional material, apparently of the same genus, from Saskatchewan. The preparation of this paper was assisted by a grant from the Marsh Fund of the National Academy of Sciences.

SYSTEMATIC DESCRIPTIONS

Genus MYTONOMYS n. gen.

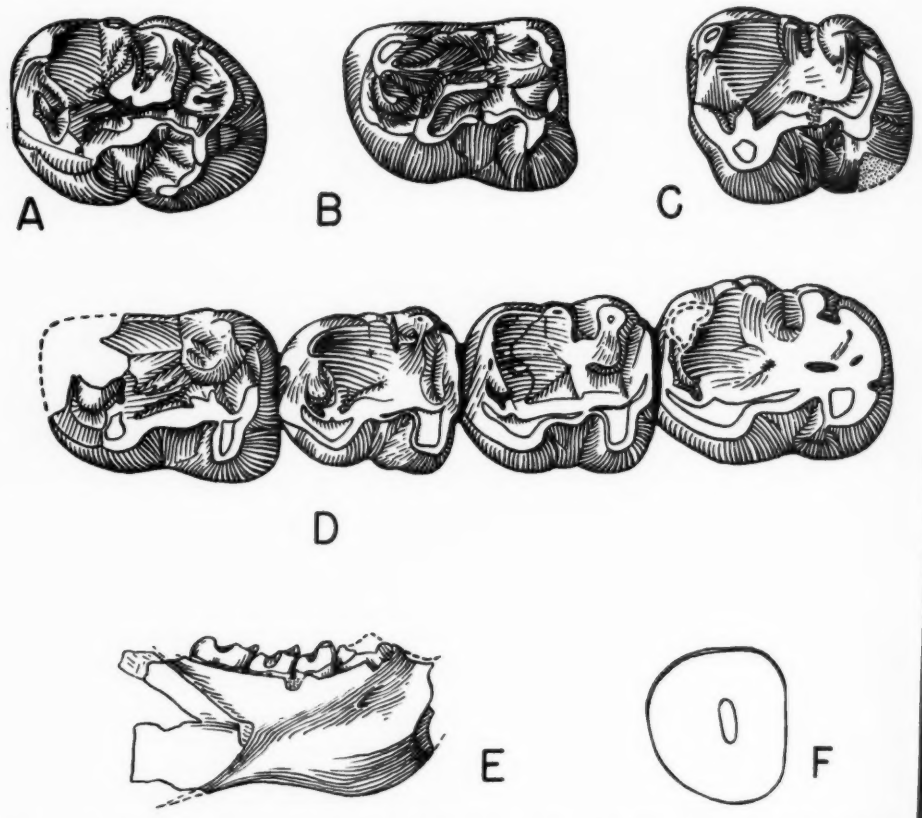
Type species.—*Prosciurus? robustus* Peterson, 1919.

Diagnosis.—Lower teeth with complicated pattern; strong broad crest from entoconid reaching to or toward the ectolophid; entoconid isolated from posterolophid; talonid basins largely obliterated; minute trigonid basins; generally a prominent mesostylid; accessory crests extend from trigonid into talonid basin; M_3 about 30% longer than M_2; lower incisor nearly equidimensional; size large.

Referred species.—*Mytonomys burkei* (Wilson) 1940.

Range.—Uintan of Utah and California.

Discussion.—This genus is related to the Oligocene *Prosciurus*, as indicated by the pattern of the lower cheek teeth, particularly by the crest from the entoconid to the ectolophid; the separation of the entoconid from the posterolophid; the large meso-



TEXT-FIG. *1*—Teeth of *Mytonomys robustus*. A. Holotype, Carnegie Mus. 2925, M_3 left ×5. B. South Dakota School of Mines 5332, P_4 left, ×5. C. Carnegie Mus. 9343, M_3 left, ×5. D. USNM 20124, P_4–M_3 left, ×5. E. Princeton Univ. 14658, lateral view of right lower jaw, ×1. F. USNM 20124, I_1 left, ×5.

stylid; the emphasis on the anterolophid and reduction of the protolophid; and the large size of M_3. The accessory crenulations (Text-fig. 1) and large size of the teeth (table of measurements) of *Mytonomys* indicate that it is not directly ancestral to *Prosciurus*. The ancestry of *Mytonomys* is not clear at present, but it is possibly descended from an undescribed middle Eocene species of *Paramys*. In another direction, *Mytonomys* is close, but not ancestral, to its contemporary *Eohaplomys* from the Sespe, the earliest known aplodontoid rodent.

MYTONOMYS ROBUSTUS (Peterson), 1919

Text-fig. 1

Prosciurus? robustus PETERSON, 1919, p. 65, fig. 6

Leptotomus? robustus (Peterson), WILSON, 1940, p. 73.

Holotype.—Carnegie Mus. 2925, fragment of the lower jaw with M_3 left.

Referred specimens.—Carnegie Mus. 2926 and 9344, Princeton Univ. 14658, USNM 20124 and 20142, and S. D. School of Mines 5332, all from the Myton Pocket; Princeton Univ. 11296 (in part) from the Wagonhound; and Carnegie Mus. 9343 (in part) from the Randlett.

Diagnosis.—As for the genus; accessory crests relatively simple, with few accessory crenulations; trigonid basin nearly obliterated by growth from metaconid; mesostylid universally present; variation as to whether trigonid or talonid of M_3 is widest; lower cheek tooth series over 23 mm. long.

MEASUREMENTS OF TEETH OF *Mytonomys robustus* (IN MM.)

	Holotype, Carnegie Mus. 2925	Range	Mean	N
P_4-M_3		23.1–23.2	23.2	2
P_4 anteroposterior		5.87	5.87	1
width, metalophid		4.30–4.35	4.33	2
width, hypolophid		4.48–4.55	4.52	2
M_1 anteroposterior		4.71–5.32	4.92	4
width, metalophid		3.95–4.05	3.99	4
width, hypolophid		4.35–4.55	4.46	4
M_2 anteroposterior		4.94–5.16	5.06	5
width, metalophid		4.26–4.69	4.52	5
width, hypolophid		4.58–4.64	4.61	3
M_3 anteroposterior	6.71	6.45–6.80	6.64	8
width, metalophid	4.92	4.72–5.13	4.96	7
width, hypolophid	5.14	4.42–5.14	4.64	8
I_1 anteroposterior		3.71–4.45	4.15	4
transverse		3.26–3.66	3.38	4

Range.—Upper Eocene Uintan of northeastern Utah.

Discussion.—This species is unfortunately known only from fragmentary lower jaws. The multiplicity of minor crests filling the central basin is well shown in unworn teeth (Text-fig. 1,A–D). With wear, as the basin is ground flat against the upper teeth, many of the irregularities disappear, although traces of them remain for a long time (Text-fig. 1,C–D). The lower tooth row, when seen from the side, is strongly concave upward (Text-fig. 1,E). The chin is prominent. The mental foramen is minute, and is set at the posterior end of a pit, so that in the text-figure (1,E) it appears to be large. But the actual foramen occupies only the posterior quarter of this groove. An unusual feature of the jaw is a very strong ridge along the lateral margin, above the alveolus of the incisor. The masseteric fossa is almost flat. The lower incisor is very wide, and the enamel is unusually thin (Text-fig. 1,F). The pulp cavity is oval.

REFERENCES

PETERSON, O. A., 1919, Report upon the material discovered in the Upper Eocene of the Uinta basin by Earl Douglass in the years 1908–1909 and by O. A. Peterson in 1912: Ann. Carnegie Mus., vol. 12, p. 40–168.

WILSON, R. W., 1940, Californian paramyid rodents: Carnegie Inst. Wash. Publ., no. 514, p. 59–83.

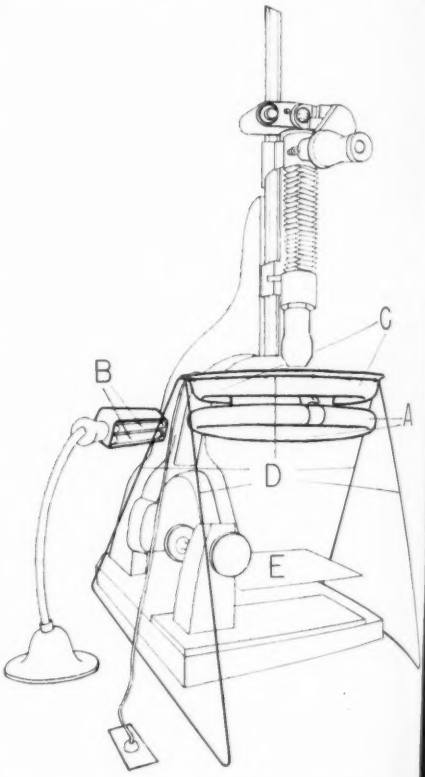
MANUSCRIPT RECEIVED OCTOBER 19, 1955

PHOTOGRAPHING SMALL FOSSILS

HARRY B. WHITTINGTON
Museum of Comparative Zoology, Harvard University

The small fossils of which I have been trying to get the best possible photographs are early growth stages of trilobites, the maximum dimension of which may be less than 1 mm., the shape hemispherical or even sub-spherical, and the external surface granulate or spinose. The aim has been to produce a picture of the fossil magnified 30 to 50 diameters. To photograph them directly at this magnification with a vertical camera is well-nigh impossible because of (a) the great bellows extension demanded with, say, a 50 mm. or longer focus lens, and (b) the tiny diaphragm aperture required to give the necessary depth of focus. I have therefore been making the negative at 10 diameters and enlarging it. This requires a sharp blemish-free, fine grained negative. To avoid dark shadows an even light over the whole surface is desirable, supplemented by a moderate north-west highlight. The focus is clearly critical—it must be as near as possible to the median plane of the object, so that when the diaphragm aperture is reduced the best use of the increased depth of focus may be obtained. A fluorescent ring light (A in Text-fig. 1) provides an ideal source of even illumination over the whole surface, and two small fluorescent tubes (B in Text-fig. 1) give the required northwest highlight. Light from fluorescent tubes has two great advantages: (1) it is clear and crisp and allows precise focussing at the right point on the specimen, and (2) the tubes do not emit heat, so that they are not only more comfortable to work with, but also the plasticine which may be used to support the specimen is not softened. Such softening, which may occur when tungsten filament or other source of illumination is used, may cause the specimen to move during a long exposure.

The apparatus shown in Text-fig. 1 is that which I prefer, but of course different types of cameras and other sizes of ring lights may be used. The camera is a "Leica," mounted on the Leitz "Aristophot" equipment, which incorporates an adequate bellows extension and a reflex mirror with a clear glass focussing screen. It is mounted on a heavy vibration-free vertical post and base. The 35 mm. frame is of adequate size for my subjects, and roll film cartridges are vastly more convenient than cut film, which must be loaded into film holders. A clear glass focussing screen, with the magnifying viewer, is essential for critical focus. The ring light (A) is a domestic ceiling fixture commonly carried by electrical supply and hardware stores, the ring 12 inches in diameter, 32 watts, and described as "standard cool white." An opening some 7 inches in diameter was made in the center of the convex metal disc (C) on which the ring is



TEXT-FIG. 1—Diagram to show the use of fluorescent tubes (A is a ring; B, two short tubes to illuminate for photographic purposes specimens placed on the adjustable table (E). (C is the metal disc on which the ring light is mounted, (D) the frame supporting it.

mounted, and this disc supported on a $\frac{1}{4}$ inch mild steel wire frame (D). The frame and disc are braced against the vertical support of the "Aristophot" to eliminate movement from side to side. If it is desired to have the height of the ring adjustable, it may be attached to sleeve clamps which run up and down vertical posts set in a horizontal base. I preferred to have the height of the ring fixed, and to move the camera. When using a lens of about 5″ focal length, for photographs at ×1 to ×3, the camera is placed about as shown in Text-fig. 1. When using a 50 mm. lens for magnifications up to ×10, the lens is mounted in an extension tube and situated below the ring (A). A lens hood should be used to exclude all but the light coming from the specimen. The extension of the camera bellows is set to determine the particular magnification, and focussing is by means of raising and lowering the specimen table (E). Vertical movement of the table must be by means of a good quality rack and pinion to allow of minute adjustments. The two 4 watt fluorescent tubes forming the highlight are mounted so that they can be screwed into an ordinary lamp socket (this "Lite-Mite Bulb" is manufactured by Stocker and Yale, Marblehead, Mass.). A goose-neck lamp affords a suitable socket, the height of which can be adjusted conveniently.

Having evolved what I find to be an ideal type of lighting, that does not demand overlong exposures, the remaining question is the type of film to be used. "Adox" film, in 35 mm. cartridges, manufactured by the Schleussner Company of Frankfurt am Main, Germany, has recently become available in this country. The emulsion layer of this film is extremely thin, effecting an increase in the resolving power over that of any other film. A discussion of the merits of Adox film, and of how it should be developed, will be found in "Leica Photography," issues for Summer and Fall, 1955 (vol. 8, nos. 2 and 3). I have found that Adox film, type KB-14, developed in the liquid formula X-22, made up by the FR Corporation, New York City, will give negatives of most exceptional resolution. Enlargements made from them show as much detail as can be reproduced (or even more than can be reproduced) by the prevailing collotype method

A TECHNIQUE OF STEREOPHOTOMICROGRAPHY FOR ILLUSTRATIONS IN MICROPALEONTOLOGY

E. P. LEHMANN
Wesleyan University, Middletown, Connecticut

ABSTRACT—The adaptation and modification of the stage of a one circle goniometer to the stage of a petrographic microscope for taking stereomicrographs of microfossils is described.

INTRODUCTION

In the course of taking routine photomicrographs for illustrating Foraminifera the writer devised simple equipment and techniques for taking them stereoptically. The encouraging results prompted the writing of this short paper, since it was felt that other micropaleontologists might also find stereomicrographs useful for illustrations.

STEREOGRAPHIC METHODS

The procedure for taking stereographs and the design of equipment necessary is well defined by Branson, Mehl & Branson (1933, p. 17) and Gott (1945). Following the procedures outlined by these authors the two components of the stereograph are obtained by a rotation of the optic axis of the lens system of the camera between the two exposures. This method has given excellent

results as can readily be seen upon examination of the illustrations accompanying these introductory papers. Evitt (1951, 1953), Evitt & Whittington (1953), and Whittington & Evitt (1954), in a series of publications concerned with the taxonomy of the trilobites have very effectively used stereographs in conjunction with conventional photographs.

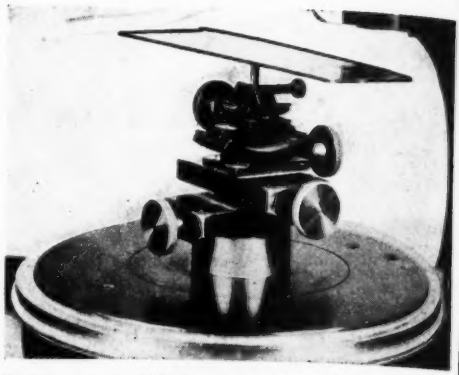
These illustrations prompted the writer to investigate the possibility of stereographs for the illustrations of some Recent Foraminifera from Matagorda Bay, Texas, which are currently being studied.

STEREOMICROGRAPHIC EQUIPMENT AND TECHNIQUE

In view of the high magnifications required for photographic illustrations of true microfossils, it is generally customary to use a microscope in conjunction with a photomicrographic camera. Consequently, the technique of rotating the axis of the optical system to obtain stereographs cannot be employed readily in the taking of stereomicrographs. The alternative system, that of rotating the specimen about an axis, however, can be accomplished by several means, one of which is described below.

By several small alterations and additions, the stage of a one circle goniometer was adapted to a petrographic microscope stage. The goniometer stage used had two arcs of rotation at right angles, which were actuated by the thrust motion of two screws. Horizontal movement parallel to either of the two arcs was accomplished by the thrust action of two additional screws. The small mounting platform of the goniometer was replaced by a brass plate measuring $10 \times 3 \times 0.1$ cm. A platform of this size allowed the conventional recessed microfossil slide to be placed in position for photography of a specimen mounted anywhere within the slide.

The goniometer stage was fixed to the microscope stage by a screw through a short brass column set into the central hole of the microscope stage plate. A circular brass plate, 0.1 cm. thick and of larger diameter than the hole in the stage, was inserted below the microscope stage and held tight against the central part of the brass column, which was the same thickness as the microscope stage, and still permitted rotation of the stage. Inasmuch as the central plate of many petrographic microscopes is easily removed, the mounting and unmounting of a modified goniometer stage of the type just described is easily accomplished. Text-fig. 1 illustrates the apparatus.



TEXT-FIG. *1*—Photograph of modified goniometer stage mounted on an American Optical Company petrographic microscope.

The angle of rotation between the two photomicrographs of a stereomicrograph may be determined by means of an ordinary protractor by calibrating the arcs of the goniometer in degrees, attaching a "pendulum type" protractor to the long edge of the stage, or devising adjustable "stops" for the arcs of the goniometer.

The most realistic relief of the stereomicrograph was obtained by using this total angle of 12° (6° inclination to each side). Stereomicrographs were taken at lesser total angles (as low as 8°), but the relief appeared insufficient; conversely, a total angle of more than 12° produced exaggerated relief in the stereomicrograph. The best operating range is apparently 12° plus or minus one or two degrees.

Whittington & Evitt (1954, p. 10) have observed that "tilting the specimen has the disadvantage that the intensity of the light and shadow on different parts is changed by the tilting, and the stereoscopic effect of the two pictures is not satisfactory." Inasmuch as stereographs do not require shadows to produce the stereoscopic effect, the objection to the "tilting of the specimen" method raised by Whittington & Evitt can be readily overcome by changing the upper left

and lower right lights to equal intensity (or nearly so), and a higher angle.

The highly polished surface of some Foraminifera may produce small high spots of light on the stereomicrographs (not in the same position on the two components of the pair), which may be slightly bothersome to some people when the pair is viewed stereoscopically. Coating the specimens with either magnesium oxide or ammonium chloride would solve the light reflection problem.

CONCLUSION

It would seem that stereomicrographs can be used to great advantage in the illustration of microfossils such as Foraminifera, Ostracoda, conodonts, etc. It should be pointed out, however, that stereomicrographs should not replace the conventional method of three photomicrographs of three different views, but used to supplement them. In some instances, by using a stereomicrograph, it may be necessary to present only one other photomicrograph of a different view. Also, either element of the stereomicrograph can serve as one of the conventional three views, and consequently using stereomicrographs would normally only increase the minimum number of illustrations per species described to four.

By combining conventional photomicrographs with stereomicrographs on one plate as demonstrated by Evitt (1949, p. 568, pl. 88), the greatest economy of space would be facilitated, and in all probability the number of plates required per paper would not be significantly increased. Evitt (1949), discusses the various applications of stereographs other than for published illustrations, suggesting their use in records, references, and teaching.

REFERENCES

BRANSON, E. B., MEHL, M. G., & BRANSON, E. R., 1933, Conodont studies: The University of Missouri Studies, vol. 8, nos. 1–4, 343 p., 28 pl.

EVITT, W. R., 1949, Stereophotography as a tool of the paleontologist, Jour. Paleont., vol. 23, p. 566–570, pl. 88.

——, 1951, Some Middle Ordovician trilobites of the families Cheiruridae, Harpidae, Lichidae: Jour. Paleont., vol. 25, p. 584–616, pl. 85–88.

——, 1953, Observations on the trilobite *Ceraurus:* Jour. Paleont., vol. 27, p. 33–48, pl. 5–8.

——, & WHITTINGTON, H. B., 1953, The exoskeleton of *Flexicalymene* (Trilobita), Jour. Paleont., vol. 27, p. 49–55, pl. 9, 10.

GOTT, P. F., 1945, Procedure of simplified stereophotography of fossils: Jour. Paleont., vol. 19, no. 4, p. 390–395, 1 pl., 9 fig.

SCHMIDT, R. A. M., 1948, Radiographic methods in paleontology, Am. Jour. Sci., vol. 246, p. 615–627, 6 pl.

WHITTINGTON, H. B., & EVITT, W. R., 1954, Silicified Middle Ordovician trilobites: Geol. Soc. Am. Mem. 59, 137 p., 33 pl.

MANUSCRIPT RECEIVED NOVEMBER 7, 1955

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 760–769, MAY 1956

NOMENCLATURAL NOTES

NOTES ON SOME ORDOVICIAN SPONGES AND THEIR NAMES

G. WINSTON SINCLAIR
Geological Survey of Canada, Ottawa

To produce such an inclusive work as the *Treatise on Invertebrate Paleontology* free from all error would require authors more than human in their capacities. Slips may be expected, and may be excused, but I think should also be corrected, since the *Treatise* will be relied on as the source of information in its field. The notes below deal with a few points which came to my attention in reading the chapter on the Porifera, by Dr. M. W. de Laubenfels. They are arranged by *Treatise* pages.

P. 60. *Microspongia* is accepted as a senior synonym of *Hindia*. This synonymy has been suggested by many students of Cincinnatian fossils, but the meagre description and figure of the older genus have prevented close comparison. If the description is correct, and *Microspongia* has needle-like spicules, then *Hindia* cannot be a synonym. It would seem that until the types of *Microspongia* can be redescribed the established genus *Hindia* should not be rejected. The type species of *Microspongia*, *M. gregaria*, is from the Cincinnatian, not the Silurian, but the figure given in the *Treatise* (fig. 44,2) is probably not of that species. Rauff (from whom it was copied by Zittel, and then by the *Treatise*) labelled it only "Ennomoclon (Trider) von *Hindia*," and it may be presumed to be, like most of Rauff's well-preserved material, from a Silurian species.

P. 61. *Caryomanon*. *Spongia incisilobata* Roemer was designated as type of this genus by Bassler in 1915. Bassler also designated type species for *Caryospongia* and *Steliella*, but in these cases he chose the same species as did de Laubenfels.

P. 64. The genotype of *Trachyum* was set by the original publication.

The type species of *Edriospongia*, *Streptosolen* and *Strotospongia* are of Ulrich & Everett, 1890. The genera themselves are correctly cited as of Miller, 1889, who extracted them from the proofs of the Illinois report which appeared the next year.

The type species of *Anthaspidella* was selected, I think, by Bassler in 1915. The doubt is because Miller in describing the genus named the then undescribed *A. mammulata* as type, a procedure I think null.

Zittelella was described by Miller, again from the Ulrich & Everett manuscript, but in this case he referred one previously described species to it (*Palaeospongia trentonensis* (Worthen 1875) = *Cnenidium ? trentonenesis*) which must be its type species by monotypy.

Dystactospongia is of Miller, 1882, and the type was set in the original publication.

Heterospongia was described from the Cincinnatian.

The type species of *Pycnopegma* was designated by Bassler in 1915, as was that of *Anomoclonella*.

P. 69. *Cyathophycus* has had a tangled history. Walcott described it as an alga, and later realized it was a sponge. Dawson agreed, and changed the name to *Cyathospongia* to indicate the relationship. Hall & Clarke replaced Dawson's homonymous name by *Cyathodictya*. All these genera had the same type species, *C. reticulatus*. Thus the entries under *Cyathodictya* (p. 72), and under *Cyathophycus*, type *C. subsphaericus*, (p. 103) are redundant.

The type species of *Megastylia* is *M. caliciformis*.

P. 70. *Halichondrites* was described by Hinde in 1888, and its type species by Dawson in Dawson & Hinde in 1889.

P. 78. Ruedemann has described species of *Pyritonema* from the Ordovician of New York.

Acanthospongia and its single species were established by McCoy in 1846, although the "provisional" nature of the designations might be held to invalidate them. However, *Acanthospongia* is included in his table of genera, and seems as well established as many others.

P. 81. The type of *Okulitchina* was set by original designation.

P. 96. The type species of *Camarocladia* is of Ulrich & Everett, 1890.

P. 104. The type species of *Cylindrocoelia* was set in the original publication.

P. 106. The type species of *Palaeospongia* is *P. cyathiformis* (not *Porites cyathiformis*), a Trenton species, by monotypy. This genus has always been considered, I think rightly, as a synonym of *Ischadites*.

P. 107. The type species of *Rauffella* was designated in the original publication.

Satratus is a myth. What Seeley did describe was a species, *S.* [*trephochetus*] *atratus*.

P. 108. *S. ocellatus* is the type species of *Strephocetus* by monotypy.

P. 110. *Receptaculites neptuni* is from the Devonian of Europe.

Dictyocrinus was described from the Devonian.

The type species of *Lepidolites* is *L. dickhauti*, by original designation.

A. reticulatus is the type species of *Anomaloides* by monotypy.

NOMENCLATURE

As readers of this Journal know, I have been most outspoken in defense of the right of an author to name a genus anything he chooses, believing as I do that good names are to be encouraged by education rather than by legislation. This belief implies that we be willing to assume the distasteful chore of protesting when names are coined which seem to us objectionable. Among the scores of new names proposed by de Laubenfels are three kinds which I would not like the young to take as examples.

Four and a half pages are devoted to a list of "Unrecognizable supposed sponges," the length of the list reflecting the great variety of dubious objects which have been placed in the group at one time or other. Five of these names, being homonyms, are replaced with new ones. The recommendation that homonyms be replaced only when study shows that the entity is a valid one without an available synonym seems to me still a wise one.

Any combination of letters may denote a genus, and every generic name, no matter how derived, is to be treated as if it were a noun in the nominative singular form. Some may find this difficult to do when the name is a word which they had learned as an adjective (e.g. *Ordinatus, Intertextum, Nitidum, Ornatus*). There are precedents, but they mostly date from an antique period in nomenclature, and I think most current workers would prefer a name which was more credibly a noun. These names are, of course, quite legal, as is the one discussed next.

The name *Sagarites* which Makiyama proposed for a genus of sponges, being preoccupied, is here (p. 39) replaced by the new name *Makiyama*. Many classical nouns end in -er, -um, or -es, but I trust I shall never see a brachiopod genus *Cooper*, read of the interesting ammonite *Kellum*, or have to refer to the solitary coral *Jones*.

MANUSCRIPT RECEIVED NOVEMBER 21, 1955

NOTES ON, AND RECTIFICATIONS OF, PELECYPOD NOMENCLATURE

H. E. VOKES
The Johns Hopkins University

ABSTRACT—Studies in preparation for the Pelecypod volume of the *Treatise on Invertebrate Paleontology* have made necessary the following nomenclatorial decisions: (1) *Tellina abildgaardiana* Spengler is type of *Gastrana* Schumacher, 1817, since *Tellina fragilis* Linné was not available; (2) *Psammobia filosa* Conrad is designated as type of *Garum* Dall, 1898; (3) The generic name *Thracia* was first published by Sowerby in 1823, and must be cited as *Thracia* Leach *in* Sowerby, 1823; the type remains *T. corbuloides* Blainville; (4) *Pandorella* Conrad, 1863 has priority over *Kennerlia* Carpenter, 1864; (5) *Eudorina* Pascher, 1926 is not available as a substitute name for *Pandorina* Scacchi, 1833 (non St. Vincent, 1827) but the latter is a synonym of *Lyonsia* Turton, and no new name is needed. (6) The type of *Cochlodesma* Couthouy, 1829 is the European *Mya praetenuis* Pennant; *Aperiploma* Habe, 1952 may be used for the West Atlantic species formerly referred to *Cochlodesma; Bontaea* Leach *in* Brown, 1844, *Bontia* Leach *in* Gray, 1847, and *Galaxura* Leach, 1852 are exact synonyms of *Cochlodesma*. (7) New names proposed are: *Thyellisca* for *Thyella* Adams, 1866 (non Wallengren, 1858); *Pteropsella* for *Pteropsis* Conrad, 1860 (non Rafinesque, 1814); and *Liopistha elegantulata* for *Cardium elegantula* Roemer, 1849 (non Beck, 1842).

During the course of studies preparatory to the compilation of certain sections of the Pelecypod volume of the *Treatise on Invertebrate Paleontology*, the writer has accumulated a number of nomenclatorial problems that require discussion at greater length than can be permitted in that work, as well as a number of homonyms that must be renamed.

GASTRANA Schumacher, 1817 (Tellinidae)

Schumacher (Essai Nouv. Syst. vers Test. 1817, pp. 44,132) recognized two divisions of his genus *Gastrana*: one, designated α, was typified by *Gastrana donacina* Schumacher, with synonymy as follows: "*Tellina Abildgaardiana* Spengl. l. c. pag. 90. No. 18. *Tellina Guinaica* Chemn. 10. pag. 348. Tab. 170. fig. 1651–1653." The other, designated β was typified by *Gastrana monstrosa* Schumacher, with synonymy: "*Venus monstrosa* Chemn. 7. pag. 50. Tab. 42 fig. 445,446.a.b." Herrmannsen, (1847, p. 463) cites: "Typus *Venus monstrosa* Chemn. and *Tellina Abildgaardiana* Spengler" while Gray (1847, p. 184) gives: "Gastrana α, *Schum.* 1817. Tellina guinaica." and "Gastrana β, *Schum.* 1817. Corbula, sp. *Brug.* Venus monstrosa."

H. & A. Adams (1856, p. 402), Fischer (1887, p. 1149), Tryon (1884, p. 171), etc. cite *Gastrana fragilis* (Linné) as example, and Stoliczka (1870, p. 120) says: "The best known species, *Gast. fragilis* of Linné, may be considered as the type of the genus." Dall (1900, p. 1002), Thiele (1934, p. 915), and Salisbury (1934, p. 76) all likewise cite *G. fragilis* as type, but that species, not being on the original list of Schumacher, is not available.

The first valid subsequent designation I have found is that of Bucquoy, Dautzenberg & Dollfus (1898, p. 684). "Type: *Gastrana donacina* Schumacher (=*Tellina Abildgaardiana* Spengler)." According to these authors, this species is "extremement voisin du *Gastrana fragilis*."

THYELLISCA Vokes, new name (Semelidae)

Although Dall, as far back as 1900 (p. 999) pointed out that the generic name *Thyella* H. Adams (1866, Zool. Soc. London, Proc. for 1865, p. 754) was preoccupied, the name has continued to be used, and no substitute seems to have been proposed. The new name *Thyellisca* is here proposed for *Thyella* Adams, not Wallengren, 1858 (Ofvers. VetenskAkad. Förh., Stockholm, vol. 15, p. 141; *Lepid.*) nor Robineau-Desvoidy, 1863 (Hist. nat. Dipt., vol. 1, p. 183; *Diptera*). The type species is *Thyella pulchra* Adams, a Recent species described from Singapore, which was the monotype of *Thyella*.

GARUM Dall (Gariidae)

In 1900, Dall (p. 975), proposed the name *Garum* for a "section" of the genus *Psammobia* "(Lam.) Bowdich" as a substitute name for *Gari* Cossmann (1886, Ann.

Soc. Malac., Belgique, vol. 21, p. 91) non Schumacher (1817), Ess. nouv. Syst. Vers Test., pp. 44,131), designating *Psammobia dutemplei* Deshayes, of the Paris Basin Eocene as type. He also (pp. 977–8) assigned the Claiborne species *Psammobia filosa* Conrad, and *P. claibornensis* Dall (then described) to this section.

Unfortunately, Dall earlier, in 1898 (p. 60), had used the name in a faunal list, referring to it the latter two species from Claiborne, but making no mention of *P. dutemplei* Deshayes. Since *P.* (*Garum*) *claibornensis* Dall was a *nomen nudum* at that time, I here designate "*Psammobia* (*Garum*) *filosa* Conrad" as type of *Garum* Dall, 1898. Since *filosa* and *dutemplei* are congeneric, the change of type species does not result in any change in the concept of *Garum*.

PTEROPSELLA Vokes, new name (Mactridae)

The thin-shelled and fragile mactrid from the Claiborne, Eocene, of Alabama, that was denominated *Pteropsis* by Conrad in 1860 (Jour. Acad. Nat. Sci., Philadelphia, [2], vol. 4, p. 296) requires a new generic name for *Pteropsis* had been used previously in Coleoptera by Rafinesque (1814, Specchio Sci., vol. 2, no. 12, p. 166). The new name *Pteropsella* is therefore here proposed, with *Lutraria papyria* Conrad, the monotype species of *Pteroposis* Conrad, as its type.

THRACIA (Thraciidae)

The generic name *Thracia* has been in almost universal use since its proposal by de Blainville in the 32nd volume of the Dictionnaire des Science Naturelles (1824, p. 347). Neave, however, lists it as: "*Thracia* Leach, 1823, in Sowerby, Min. Conch., 5 (72), 20." Checking this reference we find that following the description of four fossil species referred to the genus *Mya*, Sowerby states: "It is impossible to say positively to what Genus these and some other fossils referred to *Mya* rightfully belong, as we cannot find the inner parts of the hinges. Several of them resemble Leach's Genus *Thracia* in having an external ligament, but that Genus is included in *Anatina* among the Myaires by Lamarck, and even the *Lutraria* has a small external ligament, although they are both arranged in families supposed to have only an internal one . . . ."

Since Sowerby said that the fossil species of *Mya* only "resemble" *Thracia*, he clearly did not assign any of them to that genus. His statement, however, that *Thracia* has an external ligament is sufficient to establish the name for nomenclatorial purposes, and it must be treated as a genus without included species. The first species to be referred to *Thracia* were by de Blainville in the Dictionnaire. Hence the genus may continue to be used in its accustomed sense but must be cited as: "*Thracia* Leach *in* Sowerby, 1823."

PANDORELLA Conrad, 1863: KENNERLIA Carpenter, 1864 (Pandoridae)

In the Proceedings of the Academy of Natural Sciences, Philadelphia, for 1862 (published Feb. 17, 1863) Conrad proposed the name *Pandorella* (p. 572) with *Pandora arenosa* Conrad (1834, p. 130) as the sole referred species. During the following year Carpenter proposed *Kennerlia* (Rep. Brit. Assoc. [Newcastle, 1863)], 594, 638; [August, 1864]), as a subgenus of *Pandora* with two original species, *K. filosa* and *K. bicarinata*. Stoliczka (1870, p. 61) designated *K. bicarinata* as type of the subgenus.

Subsequently, in 1867 (p. 269), Conrad made the following statement: "*P*[*andora*] *arenosa* Con. (*Pandorella* Con.) is a true *Pandora*, and therefore the genus *Pandorella* is eliminated." This statement was accepted without question by Stoliczka (1870, p. 62) and subsequent authors, Dall (1903, p. 1518) even going so far as to state: "*Pandorella*, *Trutina*, and *Calopodium* are exact synonyms of *Pandora* s.s." On the same page he refers *P. arenosa* to the subgenus "*Kennerleyia*," a procedure that has been accepted by all subsequent authors.

It is obvious of course that Conrad was in error in 1867 in "eliminating" *Pandorella* as a synonym of *Pandora* s.s., as typified by the European *P. inaequivalvis* (Linnaeus), a species that has been well figured by Bucquoy, Dautzenberg and Dollfus (1898, p. 723, pl. 98, figs. 1–6). In terms of modern conchology, *Pandorella* is a valid subgenus of *Pandora* and has priority over *Kennerlia* Carpenter.

PANDORINA Scacchi, 1833 (Lyonsiidae)

Neave, in volume 3 of his Nomenclature Zoologicus (p. 564) lists: "*Pandorina* Scac-

chi, 1833, Osserv. Zool., 15.-Moll. (See *Eudarina* Pascher, 1926)." The name *Eudarina* does not occur, but under *Eudorina* we find: "*Eudorina* (n.n. pro *Pandorina* Scacchi) Pascher, 1926, Arch. Protistenk., 53, 470, 471.—Prot." Since *Pandorina* Schacchi was preoccupied by *Pandorina* Bory de St. Vincent, 1827 (Encycl. Meth. (Zooph.), p. 600, *Protozoa*) a check was made of the Pascher work. Here *Eudorina* is used for a protozoan, appearing as "*Eudorina charkowiensis* nov. comb. (*Pandorina charkowiensis* Korschikoff)". There is no indication that *Eudorina* is proposed as a new name, apparently being used as originally proposed by Ehrenberg in 1832 (Preuss. Akad. Wiss., Abh., 1832, p. 78). It clearly was not considered by Pascher as a substitute name for *Pandorina* Scacchi.

Tellina corruscans Scacchi, the sole species referred by Scacchi to *Pandorina* is considered by Bucquoy, Dautzenberg and Dollfus (1898, p. 730) to represent a variety of *Lyonsia norvegica* "Chemnitz" [Gmelin], the type of *Lyonsia* Turton, 1822 (Conch. Insul. Brit., p. 35). In that work Turton listed but one species under the genus *Lyonsia*. This he denominated as *Lyonsia striata*, with *Mya striata* Montagu, *M. pellucida* Brown, and *M. norvegica* Gmelin in the synonymy. The latter name has priority, and was cited as type by Gray (1847, p. 191). There is, therefore, no need of a substitute name for *Pandorina* Scacchi.

COCHLODESMA Couthouy—APERIPLOMA Habe (Periplomatidae)

The genus *Cochlodesma* Couthouy (1829, Boston Jour. Nat. Hist., vol. 2, no. 2, p. 170) is usually cited as having as its type, by monotypy, *Anatina leana* Conrad, a Recent west Atlantic species. Grant & Gale (1931, p. 255, footnote) however, state: "Couthouy placed '*Anatina Leana* Conrad' in this new genus, including '*Mya praetenuis* Pennant' as a synonym of his type. Gray, 1847, fixed the type on Pennant's species."

Examination of the original proposal shows that neither point of view is correct, for *Cochlodesma* is not monotypic, and '*Mya praetenuis*' was not placed in the synonymy of *C. leana*. Instead, we find, after the citation of *C. leana*, the following:

> *Observations:* The figures and descriptions by British authors of CHAMA *praetenuis*, Petiver, MYA *praetenuis*, Pennant, Donovan, Wood, Dillwyn, Turton (Conch. Dict.), LIGULA *praetenuis*, Turton (Bivalves) and Brown, seems to answer so closely to Mr. Conrad's shell that it appears doubtful to me whether they are not identical. . . . If the *praetenuis* prove specifically distinct from the *Leana*, there is no doubt of it being generically the same . . .

Hence, there can be no question as to the availability of *M. praetenuis* for subsequent designation as type of *Cochlodesma*, as was done by Gray (1847, p. 190–191). As a result, the generic name *Cochlodesma* has to be transferred from the west Atlantic species to the European form. The name *Aperiploma* Habe, 1952 (Gen. Jap. Shells, Pelecypoda, no. 3, p. 265) with *Cochlodesma leana* "Conthouy," as type by original designation, is available as a substitute.

Fischer (1887, p. 1170), Thiele (1934, p. 941) and others have considered *M. praetenuis* to be subgenerically distinct from *Cochlodesma* as typified by *C. leana* (Conrad). They have used *Bontaea* (Leach MS) Brown, 1844 (Illust. Conch. Great Britain and Ireland, 2nd ed., p. 106) as the name for the group. Brown used the generic name *Ligula* Montagu, 1808 (Test. Brit., Suppl., p. 22) with *Bontaea* in the synonymy of *Ligula praetenuis* as "Bontaea praetenuis, Leach, MSS., p. 6." Gray (1847, p. 190) used the name as "*Bontia* Leach MSS., 1818, Brown, 1844," with *Mya praetenuis* as type, but when the Leach manuscript was finally published in 1852 that species given as the monotype of *Galaxura* Leach (Synopsis Moll. Great Britain., pp. 267,271). These must now be considered as synonyms of *Cochlodesma*.

LIOPISTHA ELEGANTULATA Vokes, new name (Poromyacidae)

Cardium elegantulum Roemer (Texas, 1849, p. 405), the type species by original designation of *Liopistha* Meek, 1864 (Smisth. Mis. Coll., no. 177, p. 12,32), was when proposed a homonym of *C. elegantulum* Beck (Naturhist. Tidsskrift. IV [1], 1842, p. 93). The new name *Liopistha elegantulata* is here proposed for Roemer's species from the Austin Chalk, Cretaceous, of Texas.

REFERENCES

ADAMS, HENRY, & ADAMS, ARTHUR, 1854-8, The genera of Recent Mollusca: vol. 2, 660 p. London.

BUCQUOY, E., DAUTZENBERG, PH., & DOLLFUS, G., 1887–1898, Les Mollusques marins du Roussillon. II. Pelécypodes: 884 p., 99 pl. Paris.

CONRAD, T. A., 1834, Descriptions of new Tertiary fossils from the Southern States: Acad. Nat. Sci., Philadelphia, Jour. (1), vol. 7, p. 130–157.

——, 1867, Description of new genera and species of Miocene shells, with notes on other fossil and recent species: Am. Jour. Conch., vol. 3, p. 257–270, pl. 19–24.

DALL, W. H., 1898, Synopsis of the Recent and Tertiary Psammobiidae of North America: Acad. Nat. Sci., Philadelphia, Proc. for 1898, p. 57–62.

——, 1900–1903, Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River: Wagner Free Inst. Sci., Trans., vol. 3, pts. 5, 6; pt. 5, p. 949–1218, pl. 36–47 (1900); pt. 6, p. 1219–1654, pl. 48–60 (1903).

FISCHER, J. P., 1880–1887, Manuel de Conchyliologie et de paléontologie conchyliologique: 1369 p., 23 pl., 1138 text-fig. Paris.

GRANT, U. S. IV, & GAYLE, H. R., 1931, Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions: San Diego Soc. Nat. Hist., Mem. I, 1036 p., 32 pl.

GRAY, J. E., 1847, A list of the genera of Recent Mollusca, their synonyma and types: Zool. Soc. London, Proc. 1847, p. 129–206.

HERRMANNSEN, A. N., 1846–47, Indicis generum malacozoorum primordia: vol. I (A–L), p. 1–637.

ROEMER, F. A., 1849, Texas, mit besonderer. Rücksicht auf deutsche Auswanderung und die physischen Verhältnisse des Landes nach eigener Beobachtung geschildert von Dr. Ferdinand Roemer: xv+464 p., 1 map, Bonn.

SALISBURY, A. E., 1934, On the nomenclature of Tellinidae, with descriptions of new species and some remarks on distribution: Malac. Soc., London, Proc., vol. 21, p. 74–91, pl. 9–13.

STOLICZKA, FERDINAND, 1870–1871, The Cretaceous fauna of Southern India. III. The Pelecypoda, with a review of all known genera of this class, fossil and Recent: Mem. Geol. Surv. India, Palaeont. Indica, ser. 6, vol. 3, p. 1–222, pl. 1–12 (1870); p. 223–538, i–xxii, pl. 29–50 (1871).

THIELE, JOHANNES, 1934, Handbuch der Systematischen Weichtierkunde: vol. 3, p. 779–1022, text-fig. 784–893. Jena.

TRYON, GEORGE W., 1884, Structural and Systematic Conchology; vol. 3, 454 p., pl. 92–140. Philadelphia.

MANUSCRIPT RECEIVED OCTOBER 10, 1955

SOME PELECYPOD ILLUSTRATIONS OF THE EFFECT OF THE COPENHAGEN DECISION DEFINING THE LIMITS OF GENERIC HOMONYMY

H. E. VOKES
The Johns Hopkins University

ABSTRACT—The action of the International Commission on Zoological Nomenclature, taken at the Copenhagen meeting of 1953 in defining the limits of generic homonymy with the ruling that "A generic name is not to be treated as a homonym of another such name if it differs from it in spelling by even one letter" clears up much confusion that has complicated nomenclatorial studies. As in all decisions concerning areas of past confusion, this ruling will result in some changes from presently accepted nomenclature. Specific examples are cited from among the Pelecypoda to illustrate factors involved: (1) *Galatea* Bruguiere, 1797, is not invalidated by *Galathea* Fabricius, 1793; *Galathea* Lamarck, 1805, *Egeria* de Roissy, 1805, *Potamophila* Sowerby, 1821, *Megadesma* Bowdich, 1822, and *Galateola* Fleming, 1828, are objective synonyms. *Aegeria* Fabricius, 1807, *Potamophilus* Germar, 1811, and *Potomophila* Swainson, 1840, are not invalidated by *Egeria* or *Potamophila*. (2) *Glycimeris* Lamarck, 1799, is not preoccupied by *Glycymeris* Da Costa, 1778, and *Panope* (or *Panopea*) Menard de la Groye, 1807, is an objective synonym. This change would result in much nomenclatorial confusion and application has been made to the International Commission requesting suspension of the rules with the suppression of *Glycimeris* Lamarck to maintain the present usage of *Panope*. (3) *Huxleyia* A. Adams 1860, is not invalidated by *Huxleya* Dyster, 1858, and there is no record of the publication of "*Huxleyia* Bowerbank"; *Cyrilla* A. Adams, 1860, is an objective synonym. (4) *Megadesmus* Sowerby, 1838, is not preoccupied by *Megadesma* Bowdich, 1822; *Pachydomus* Morris, 1845, is an objective synonym. (5) *Montrouzieria* Souverbie, 1863, is not invalidated by *Montrouziera* Bigot, 1860; *Eumontrouziera* Hedley, 1915, is an objective synonym. (6) *Netastoma* Carpenter, 1864, is not preoccupied by *Nettastoma* Rafinesque, 1810; *Nettastomella* Carpenter, 1865, is an objective synonym. (7) *Pristes* Carpenter, 1864, is not preoccupied by *Pristis* Link, 1790; *Pristiphora* Carpenter, 1866 (non Latreille, 1810), and *Serridens* Dall, 1899, are objective synonyms.

The action of the International Commission on Zoological Nomenclature, taken at the Copenhagen meeting of 1953, in defining the limits of generic homonymy with the ruling that: "A generic name is not to be treated as a homonym of another such name if it differs from it in spelling by even one letter" (Hemming, 1953, p. 78) has served to clear up much irritating uncertainty that has previously complicated this field of nomenclatorial study. Until this definition was promulgated there was no clear statement as to the extent of the differences that would serve to distinguish two generic names, and there was a resultant diversity of opinion and action with respect to the status of similar appearing names, especially if these were based upon the same root form. Consequently many names have been pronounced to be, and have been treated as, homonyms that are under the Copenhagen ruling sufficiently distinct to be valid entities in zoological nomenclature. Library research during the preparation of parts of the Pelecypoda volume for the *Treatise on Invertebrate Paleontology* has revealed a considerable number of instances whereby current nomenclature will be affected. Most are of interest to specialists in limited areas only; a few, however, are of sufficient interest to merit wider publication, which will, at the same time, serve to call the attention of students to the importance of this ruling. (References to the original publication of the generic names mentioned will be found in Neave's Nomenclator Zoologicus.)

1. *Galatea* Bruguière, 1797, is not preoccupied by *Galathea* Fabricius, 1793 (*Crustacea*). The name *Galatea* was used by Bruguière as a heading on plate 250 of the Encyclopedie Methodique, Historie Naturelle des Vers. Under the name were four views of a single species which Lamarck, in 1805, identified as "*Galathea*" *radiata* Lamarck, this species thus becoming type, by monotypy, of *Galatea* Bruguière. The emendation *Galathea*, of Lamarck, is invalid, being preoccupied by Fabricius' name. In the same year, 1805, de Roissy replaced *Galathea* Lamarck with *Egeria*. In 1821, Sowerby proposed to substitute *Potamophila* for *Galathea* "Bruguière," and in 1822 Bowdich nominated *Megadesma* for the same purpose. In addition, the nude name *Galateola* Fleming, 1828, has been interpreted (Herrmannsen, 1846, p. 338) as also representing a substitute name for *Galatea* Bruguière.

Under the provisions of the Copenhagen decision, the generic names *Galathea* Lamarck, non Fabricius, *Egeria* de Roissy, *Potamophila* Sowerby, *Megadesma* Bowdich, and *Galateola* Fleming are to be considered as objective synonyms of *Galatea*.

Despite the early interpretation of *Galatea* as unavailable by reason of homonymy, it has continued to be used by most authors for the fresh-water species from the West African and Nile river systems. This is well-documented by the extensive synonymy given by Germain (1918) for *G. paradoxa* (Born), the presently accepted name for the species called *radiata* by Lamarck. Thirty-nine references are given for the period subsequent to the proposal of *Galathea*. *Egeria*, *Potamophila* and *Megadesma* each appear but twice, and the few remaining citations were to such inapplicable names as *Venus*, *Tellina*, *Donax*, etc. Although Dall (1903, p. 1453), and more recently, Thiele (1934, p. 907) have used *Egeria* de Roissy as the correct name, considering *Galatea* preoccupied, the overwhelmingly predominant usage, indicated above, forecasts no unusual degree of confusion by the return to the sanctioned usage of that name.

It is pertinent to the purpose of the present paper to point out that the name *Egeria* de Roissy does not invalidate *Aegeria* Fabricius 1807 (Lepidoptera), nor does *Potamophilus* Germar 1811 (Coleoptera) invalidate *Potamophila* Sowerby, and neither of these will affect *Potomophila* Swainson 1840 (Gastropoda).

2. *Glycimeris* Lamarck 1799 is not preoccupied by *Glycymeris* Da Costa 1778 and *Panope* Ménard de la Groye 1807, is an objective synonym. This application of the Copenhagen decision would have such far-reaching results in the nomenclature of the Tertiary and Recent Pelecypoda that application has been made to The International Commission on Zoological Nomenclature requesting the use of the plenary powers to suspend the Rules in order to preserve *Panope* in the sense in which it has been used for almost 150 years.

Lamarck in 1799 proposed the generic

name *Glycimeris*, with *Mya glycimeris* Born, listed as the sole example, becoming type by monotypy. In 1801, however, in his "Systeme" he cited *Glycimeris incrassata* Lamarck (= *Mya siliqua* Spengler) as an example of the genus, and the name was applied in this latter sense by nearly all subsequent authors of the nineteenth century. *Cyrtodaria* Reuss, 1801, appears to be the correct name for this group, as "*Cyrtodaria* Daudin, 1799" commonly cited, is not available, having been used only in the vernacular "Cyrtodaire" by Daudin.

In 1807, Ménard de la Groye, proposed the name *Panope*, for two species, *P. aldrovandi* (Recent) and *P. faujasi* (fossil), both of which are now generally held to be synonymous with *Mya glycimeris* Born, the type of *Glycimeris* Lamarck, 1799. In the original publication of the name only the spelling *Panope* was used. This was in a separate pamphlet in small quarto, of thirty-seven pages and one plate, with a separate title-page dated January, 1807. On the title page, however, it is said that the paper would appear in the February, 1807, issue of the Annales of the Museum d'Histoire Naturelle de Paris. It did not appear, however, until the March-April issue of the Annales, and in that publication the spelling was *Panopea;* furthermore, the title was somewhat altered and the paper condensed from the original thirty-seven pages to nine.

Under the provisions of the International Rules of Zoological Nomenclature the distribution of separates in advance of the issuance of the book or paper to which they appertain, does not constitute publication of any new names contained therein. The evidence of the title page of the January memoir of de la Groye indicates that it was regarded as being an advanced publication, or preprint, of the paper to appear in the Annales. The change in the spelling of the generic name, the shortening of the title of the memoir, and the drastic condensation of the latter, however, make the original publication clearly not a preprint, or separate, and would seem to establish *Panope* as the valid original spelling of the name. To further substantiate this as the intended spelling is the fact that Ménard used this form in an article in the Journal de Physique published in August, 1807 (vol. 65, p. 114). The same spelling was also used by Lamarck in his "Extrait du Cours de Zoologie" (p. 108) in 1812, and by Bosc in the "Nouveau Dictionaire d'Historie Naturelle" (vol. 24, p. 466) in 1818.

In the latter year, however, Lamarck introduced the spelling *Panopaea*, apparently as an emendation of the original. He also used the name *Glycimeris* in the same sense as in 1801. In this he was followed by nearly all authors of the nineteenth century, and we have, as a result, the use of "*Panopaea*" and *Glycimeris* as genera in the same family, usually denominated as Glycimeridae, following Deshayes' proposal of that name in 1839.

In 1898, however, Dall (p. 571–572, 607–613) called attention to the generic name *Glycymeris* Da Costa 1778, as having priority over *Pectunculus* Lamarck, 1799, in the Arcidae. Furthermore, the generic name *Pectunculus* had also been used by Da Costa in 1778, and *Pectunculus* Lamarck was a homonym. The result was the rapid substitution of *Glycymeris* for *Pectunculus*, and of *Cyrtodaria* for *Glycimeris* in the Lamarckian sense of 1801; it being generally considered that the spelling *Glycimeris* was invalidated by the older *Glycymeris*.

The effect of the Copenhagen ruling would be to validate the Lamarckian spelling of *Glycimeris* as validly different from that of Da Costa's *Glycymeris*. But it would not restore it to the usage prevalent during the last century following Lamarck, 1801, but rather would displace the well-known name *Panope*, which in various spellings, has been almost universally accepted for 150 years. The International Commission on Zoological Nomenclature has, therefore, been petitioned to suspend the Rules, in order to validate Ménard's name by rejecting *Glycimeris* Lamarck, 1799, for purposes of the Law of Priority, but not for those of the Law of Homonymy. This will serve also to invalidate *Glycimeris* Lamarck, 1801, as a homonym of *Glycimeris* Lamarck, 1799. Furthermore, a ruling as to the correct spelling of *Panope* (or *Panopea*) has been requested.

3. *Huxleyia* A. Adams, 1860, is not preoccupied by *Huxleya* Dyster, 1858, (Bryozoa)

and *Cyrilla* A. Adams, 1860, is an objective synonym.

In April, 1860, A. Adams proposed the generic name *Huxleyia* for *H. sulcata*, a small pelecypod species then described from the Straits of Korea. In June of the same year he proposed the new name *Cyrilla*, saying: "In a former paper I gave the name *Huxleyia* to a new genus of bivalve mollusca. Should, however, this name have been already used, which is not improbable, *Cyrilla* might be subsituted for it." In 1868 (p. 42) he further commented: "Je l'avais nommé d'abord, d'après le professeur Huxley . . . mais j'ai dû changer ce nom en apprenant, plus tard, que M. Bowerbank l'avait déjà employé précédemment pour une Spongiaire." Search of all available sources has not revealed any genus *Huxleyia* Bowerbank. The spelling *Huxleya* as employed in Bryozoa by Dyster in 1858, and in Protozoa by Claparede and Lachmann, also in 1858, does not invalidate *Huxleyia* Adams. Since there appear to be but four species, all of the Recent fauna and all rarely represented in collections, that are correctly referable to *Huxleyia*, there seems no valid basis for requesting suspension of the rules to save the name *Cyrilla*. *Diabolica* Jousseaume, 1897, and *Cyrillista* Iredale, 1929, are synonyms of *Huxleyia*.

4. *Megadesmus* Sowerby, 1838, proposed for a Devonian species from Australia, is not preoccupied by *Megadesma* Bowdich, 1822, (see discussion of *Galatea*, above), and *Pachydomus* Morris, 1845, is an objective synonym.

5. *Montrouzieria* Souverbie, 1863, proposed for a small semelid pelecypod from the southwestern Pacific, is not preoccupied by *Montrouziera* Bigot, 1860, (Diptera), and *Eumontrouziera* Hedley, 1915, is an objective synonym.

Souverbie proposed the generic name *Montrouziera* in the Journal de Conchyliologie in 1863 (p. 282), but immediately emended, or corrected it to read *Montrouzieria* (pp. 284, 410). In the initial spelling the name was preoccupied by Bigot's usage of 1860; the emended spelling may, however, be interpreted as the first validly proposed substitute name, and hence has priority over *Eumontrouziera* of Hedley.

6. *Netastoma* Carpenter, 1864, proposed as a subgenus of *Pholas* with *P. darwinii* Sowerby from the southeastern Pacific as monotypic species, is not preoccupied, as was believed by Carpenter, by *Nettastoma* Rafinesque, 1810, (Pisces), and substitute name *Nettastomella* Carpenter, 1865, is to be considered as an objective synonym.

7. *Pristes* Carpenter, 1864, proposed for *Pristes oblongus*, a minute leptonid species from Southern California, is not preoccupied by *Pristis* Linck, 1790, (Pisces), and *Pristiphora* Carpenter, 1866 (non Latreille, 1810, Hymenoptera), and *Serridens* Dall, 1899 are objective symonyms. Dall stated (1900, p. 1156): "In 1864 (Suppl. Rep. Br. Assoc. for 1863, p. 611, 643) Carpenter used the name *Pristes* for an undescribed species of shell allied to *Rochefortia*, but when he came to describe it, regarding *Pristes* as preoccupied (Latham, 1794), he proposed the name *Pristiphora* . . . which was also unavailable." In his original usage of *Pristes*, however, Carpenter states (p. 643) "*Pristes oblongus*, n.g., n.s. Like *Tellimya* with long marginal teeth, serrated near hinge." On p. 611 he gives the locality as San Diego. The description, although very brief, was sufficient to characterize the genus and species, and *Pristes* must be considered as available from the original proposal.

BIBLIOGRAPHY

ADAMS, ARTHUR, 1868, Note sur quelques nouveaux genres de Mollusques du Japon: Jour. de Conch., vol. 16, p. 40–56, pl. 4.

DALL, W. H., 1898–1903, Contributions to the Tertiary Fauna of Florida, (etc): Wagner Free Inst. Sci., Trans., vol. 3, pt. 4, p. 571–947, pl. 23–25, "April" [October] 1898; pt. 5, p. 948–1218, pl. 36–47, December, 1900; pt. 6, p. vii–xiv, 1219–1654, pl. 48–60, October, 1903.

GERMAIN, LOUIS, 1918, Contributions a la faune malacologique de l'Afrique equatoriale. XLIX: Sur le *Galatea radiata* de Lamarck: Mus. d'Hist. nat., Paris, Bull., 1918, p. 125–136, pl. 3.

HEMMING, FRANCIS, 1953, Copenhagen decisions on zoological nomenclature; additions to, and modifications of, the Regles Internationales de la Nomenclature Zoologique: xxix+135 p., 2 pl. London.

HERRMANNSEN, A. N., 1846–1847, Indicus generum malacozoorum primordia: vol. 1 (A–L), p. 1–637. Kassel.

THIELE, JOHANNES, 1934, Handbuch der systematischen Weichtierkunde: vol. 3, p. 779–1022, fig. 784–893, Jena.

MANUSCRIPT RECEIVED JANUARY 16, 1956

PUSTULATIA, NEW NAME FOR THE DEVONIAN BRACHIOPOD *PUSTULINA*, PREOCCUPIED

G. ARTHUR COOPER
U. S. National Museum

I am greatly indebted to Mr. John A. Talent, Geology Department, University of Melbourne, Victoria, Australia, for calling to my attention that *Pustulina* Cooper, 1942 (Brachiopoda), is preoccupied by *Pustulina* (Crustacea) Quenstedt, 1857, Der Jura, Tübingen, p. 807. The copy of Der Jura in the U. S. National Museum is dated 1858. I propose therefore to substitute the name *Pustulatia* for *Pustulina* Cooper, 1942. The type species remains *Vitulina pustulosa* Hall, 13th Rep. New York State Cab. Nat. Hist., p. 72, 82, fig. 1,2, (on p. 72) 1860.

CORRECTION

In the recent article by Marvin L. Smith, "Some ostracods from the Middle Devonian Ledyard and Wanakah members of the Ludlowville formation of western New York" (*Jour. Paleont.*, vol. 30, p. 1–8, pl. 1), the following corrections and additions should be noted: On page 5, the holotype of *Amphizona pseudocarinata* Smith, 1956, was collected at locality 1 (rather than 7) and was rare at localities 1 and 5 (rather than 7). On Table 1, occurrence of *Amphizona pseudocarinata* should be indicated in sample 3 of locality 1.

NOTICES

A new list of sales publications has been compiled by the New York State Museum and is available without charge on request to the Museum at Albany 1, New York. The revised list includes a considerable number of geological and paleontological bulletins, circulars, etc., that were formerly considered out of print and have been available only through dealers. The stock of some of these items is small; in such cases, preference will be given to orders from libraries of universities, foundations and other organizations.

TREATISE ON INVERTEBRATE PALEONTOLOGY

The following parts of the TREATISE ON INVERTEBRATE PALEONTOLOGY are available as cloth-bound volumes from: The Geological Society of America, 419 West 117th Street, New York 27, N. Y.

Part D: PROTISTA $3.00
Part E: ARCHAEOCYATHA AND PORIFERA $3.00
Part G: BRYOZOA $3.00
Part P: CHELICERATA $3.50
Part V: GRAPTOLITHINA $3.00

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, P. 770, MAY 1956

SOCIETY RECORDS AND ACTIVITIES

NOMINATIONS FOR MEMBERSHIP

In accordance with Article 3, Chapter 1 of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society. The list has been approved by the Council of the Society.

COLLETTE, WILLIAM J., JR., Campus Homes No. 8, Univ. Cincinnati, Cincinnati 21, Ohio: Harold K. Brooks, John K. Pope.

DONEY, HUGH HOLT, Geol. Dept., Univ. Texas, Austin, Texas: W. C. Bell, Keith Young.

ECHOLS, DOROTHY JUNG, Dept. Geology, Washington Univ., St. Louis, Mo.: Arthur R. Cleaves, Courtney Werner.

GILL, CARL EDWARD, 725 Barney Ave., Cincinnati 15, Ohio: Harold L. Brooks, John K. Pope.

HIGGINS, MAURICE JOSEPH, JR., Shell Oil Co., P. O. Box 1861, Corpus Christi, Texas: Theodore D. Cook, A. Richard Campbell.

HILL, WAYNE NOE, Apartment 106, 6924 Millbook, St. Louis, Mo: Arthur B. Cleaves, Courtney Werner.

HOROWITZ, ALAN STANLEY, 2440 Winchester Ave., Ashland, Kentucky: J. J. Galloway, Aurele LaRocque, Harold K. Brooks.

MOLANDER, GENE EMERY, Dept. Paleont., Univ. California, Berkeley, California: R. L. Langenheim, Jr., William W. Fairchild, Joseph H. Peck, Jr.

NELSON, CLEMENS A., Geol. Dept., Univ. California, Los Angeles, Calif.: U. S. Grant, Daniel I. Axelrod, Alexander Stoyanow.

SANDERS, JOHN ESSINGTON, 2161 Yale Station, New Haven, Conn.: G. Arthur Cooper, Carl O. Dunbar, H. B. Whittington.

SHAW, WILLIAM G., Sun Oil Co., 503 N. Central Expressway, Richardson, Texas: R. J. Cordell, W. W. Schell.

TAYLOR, PETER WALTER, Shell Oil Co., P. O. Box 100, Calgary, Alberta: Gilbert O. Raasch, Grace A. Stewart.

TREXLER, DAVID WILLIAM, 1688 S. Patton Court, Denver 19, Colorado: H. E. Vokes, Thomas W. Amsden, W. A. Cobban.

ZIMMERMAN, DONALD A., 503 N. Central Expressway, Richardson, Texas: R. J. Cordell, R. C. Weart, Wm. W. Schell.

LOVEJOY, DONALD WALKER, Burying Hill Rd., Greenwich, Connecticut: Marshall Kay, Norman D. Newell, John Imbrie.

MINOPRIO, JOSE LUIS DANIEL, Patricias Mendocinas 771, Mendoza, Argentina: G. G. Simpson, Donald F. Squires.

PELTIER, EDWARD JOSEPH, Dept. Geol., Univ. Kansas, Lawrence, Kansas: Walter Youngquist, M. L. Thompson.

PINTO, IRAJÁ DAMIANI, Instituto Ciências Naturais Av. Paulo Gama-Porto Alegro, Brasil: Helen Duncan, Mackenzie Gordon, Jr., James Steele Williams.

TURCO, CAROLINE ANN, 799 Secaucus Rd., Jersey City 7, N. J.: Aurèle La Rocque, Malcolm P. Weiss, Walter C. Sweet.

WARNER, EARL, JR., 1510 King Ave., Apt. A, Columbus, Ohio.: Malcolm P. Weiss, Aurèle La Rocque, Walter C. Sweet.

WILKIE, LORNA CHRISTINE, 302 North Main St., Bellbrook, Ohio: Aurèle La Rocque, Malcolm P. Weiss, Walter C. Sweet.

JOURNAL OF PALEONTOLOGY, VOL. 30, NO. 3, PP. 771–772, MAY 1956

SOCIETY NOTES AND COMMENT

ANNOUNCEMENT OF POLICY ON THE USE OF STEREOGRAPHS IN MANUSCRIPTS SUBMITTED TO THE PALEONTOLOGICAL SOCIETY FOR PUBLICATION IN THE JOURNAL OF PALEONTOLOGY

During the past few years an increasing number of manuscripts submitted to the Paleontological Society editor have been illustrated with plates bearing stereographs (i.e., mounted stereoscopic pairs of photographs). A number of these papers have been published recently or are currently "in the mill." Although published stereographs may have certain advantages over single conventional photographs, they are considerably more expensive (two to two and a half times) by virtue of the precise positioning and the additional space required, and their number, size, spacing and arrangement raise a variety of problems for the editor and sponsoring society which are not presented by single photos.

To date there has been no established policy regarding the use of stereographs in the *Journal of Paleontology*. Feeling that some Society policy on this matter is desirable (even aside from the economics of the situation, which make a policy imperative) and convinced, furthermore that any such policy should be founded upon a broad base of opinion, the Paleontological Society editor drew up a questionnaire relating to the use of stereographs. This was submitted to 60 leading paleontologists in the United States and abroad, including specialists in a wide variety of fossil organisms. The questions were designed to secure (a) each individual's opinion regarding the use of stereoscopic illustrations in papers dealing with his specialty, and (b) an expression of opinion regarding the use, number, and arrangement of stereographs, which could serve as the basis for a policy to be applied to manuscripts submitted to the Paleontological Society for publication in the *Journal*.

Of course, the opinions of specialists regarding the value of stereographs for illustrating fossils within their special fields vary widely. Obviously, no one illustrative technique is ideal for all subjects. Thus, for some specimens stereographs may be advantageous, whereas their use for others is pointless. A few individuals expressed the opinion that any published stereograph is a luxury. However, most (70%) of those responding felt that the use of stereographs should be generally encouraged in accordance with each author's own appraisal of the value of stereographs versus single photos, and limited by the budgetary considerations of the Society.

Accordingly, authors contemplating the preparation of manuscripts for publication by the Paleontological Society in the *Journal of Paleontology* are encouraged to consider the use of stereographs among the other various means available for illustrating paleontological papers. However, use of stereographs should be guided and tempered by the recommendations below. These specific recommendations to authors reflect the opinion of the vast majority of those responding to the questionnaire and are in line with all significant editorial considerations. They will constitute a definite policy of the Paleontological Society regarding the use of stereographs for illustrations in the *Journal*. The policy set forth here will be modified as warranted by considerations based upon the growing experience of authors, editors and readers with stereographs. In no sense is the policy intended to dictate how authors shall illustrate their papers, but only to establish principles aimed at insuring that the plates utilizing stereographs in this *Journal* are of uniformly high caliber and of maximum value to the greatest number of paleontologists, while still being economically feasible.

If an author chooses to use stereo pairs for illustrating a paper, it is recommended that—

1. Stereographs should be limited to significant selected views supplementing single conventional photographs.
2. Stereographs and single photos should be arranged in combination on a plate so as to achieve the greatest economy of space.
3. If a given specimen would normally require more than one view to be illustrated adequately by single photos, then one stereo pair should not be used

as a sole substitute for all the views.

4. The standard distance between similar points on the two elements of a stereograph should be 2½ inches; under no circumstances should the distance exceed 2¾ inches. (This approximates the average interpupillary distance, assuring that most individuals can view the stereograph readily with a simple and inexpensive pocket stereoscope, or without a stereoscope).
5. If the angular parallax in a stereograph is achieved by a procedure involving movement of the specimen while the camera remains stationary, then illumination should be such that strong shadows or highlights do not appear in different positions on the specimen in the two elements of the stereo pair.

RECENT BOOK

JURASSIC GEOLOGY OF THE WORLD by W. J. Arkell (Oliver and Boyd, Edinburgh and London, 1956; $16.50).

The following is quoted from the publishers' leaflet:

"After an introductory chapter explaining the classification used, the general geological relations of the Jurassic system in each area are described, followed by a tabulated statement, stage by stage, of the faunas and rock-types present. Correlations are based throughout on critical assessment of the ammonites. The author has considered all evidence known to him, to the end of 1954. Thus, the major part of the book is arranged geographically as a reference work. Page headings facilitate rapid explorations of the text. There are 28 correlation tables.

"In the 'General Survey and Conclusions' the stratigraphical data are sifted for evidence on fundamental geological problems such as permanence of oceans, continental drift, faunal realms, climate, geosynclines, and the distribution and chronology of volcanism and crustal deformation. When reviewed in the light of the more refined stratigraphy now available, the problems are more clearly seen and some deductions are possible.

"There are 30 plates of photographs of Jurassic outcrops and scenery, and 16 plates illustrating zonal index species of ammonites, wherever possible from the type specimen. The bibliography of about 2800 references is arranged by regions corresponding with the text."

Contents comprise: Introduction (11 p.), Western and Southern Europe (234 p.), Africa and Arabia (88 p.), Southern Asia (95 p.), Australasia (17 p.), Northeastern Europe and Northern Asia (52 p.), America and Antarctica (71 p.), General Survey and Conclusions (46 p.), Bibliography (114 p.), Zonal Index Ammonites (33 p.), Index (11 p.)

REQUEST FROM CZECHOSLOVAKIA

The State Geological Survey of Czechoslovakia writes from Prague to ask if the Paleontological Society is interested in exchanging recent volumes of our *Journal* for their publications. The Society is not able to do this, but would any university geology department wish to undertake it? At Prague they have volumes 15–26 and 28 (some incomplete) of our *Journal*, but are unable to purchase old volumes or current ones. Nowhere in Czechoslovakia is a complete set of our *Journal* available. They offer for an exchange articles on geology, paleontology (including Pleistocene) and stratigraphy. Most of the papers have English translations. For further details write to the Society Secretary.

HARPER & BROTHERS PUBLISHERS

ARE PLEASED TO ANNOUNCE THE PUBLICATION
OF AN IMPORTANT WORK FOR PALEONTOLOGISTS

INTRODUCTION
to
MICROFOSSILS

By DANIEL J. JONES

ASSOCIATE PROFESSOR OF GEOLOGY, UNIVERSITY OF UTAH

This outstanding new volume is the only work now available on a subject of great importance to geologists. In it the author describes (1) methods of collecting, separating, and mounting microfossils, and (2) micropaleontological objects representing all major groups of the plant and animal kingdom. Special attention is devoted to plant microfossils, especially the spores and pollens, which are becoming increasingly important in exploration geology. There are full discussions of the environmental significance of various microfossils and the applications of micropaleontological data to practical problems in economics and geology. The text is thoroughly documented and the lavish illustrations are outstanding.

406 pages *$6.50*

HARPER & BROTHERS

49 East 33d Street New York 16, New York

ENGINEERED BY SCHLUMBERGER!

THE SUPER-JET

A COMPLETELY NEW EXPENDABLE SHAPED CHARGE PERFORATOR WITH GREATLY INCREASED PENETRATING POWER

SCHLUMBERGER—the originator of the Expendable Shaped Charge Perforator—is proud to announce two models of a new expendable gun for use in permanent well completions through 2-inch and 2½-inch tubing. A gun more rugged and powerful than any other in the field, The Super-Jet offers the industry unequaled advantages at no increase in perforating costs:

Superior Penetration—The Super-Jet is more powerful and makes a cleaner hole than any other expendable perforator.

Simple Rugged Construction—The charges are contained in a thin-walled tubular carrier which is strong enough to permit spudding.

Charges Are Always in Firing Position—If shooting depth can be reached, the Super-Jet can be fired.

Does Not Require Delicate Handling—Long-gun sections can be run as easily as short ones.

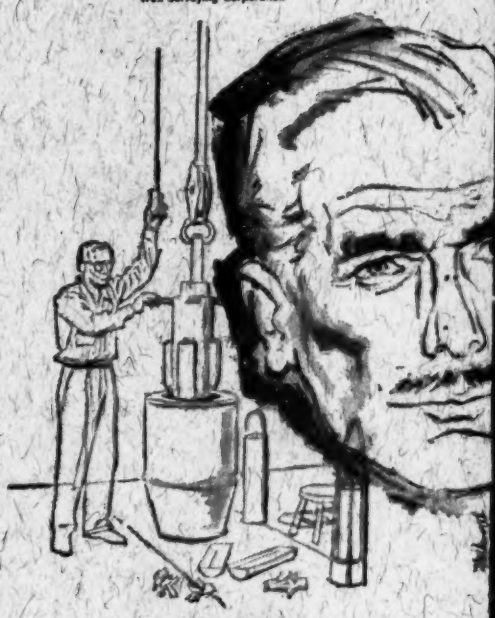
Engineered for Complete Safety—The Super-Jet gun will not fire if well-bore fluid enters the carrier.

For the Best in Perforating Performance

Call

SCHLUMBERGER

Well Surveying Corporation



THE EYES OF THE OIL INDUSTRY